FEEDING ECOLOGY OF SCAUP DUCKLINGS ACROSS A HETEROGENEOUS BOREAL WETLAND LANDSCAPE

By

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Abstract

Understanding how patterns of food resources influence the behavior and fitness of free-living animals is critical in predicting how changes to such resources might influence populations. The boreal region of North America is relatively undeveloped and contains abundant freshwater lakes and wetlands. These largely pristine and stable habitats harbor high densities of aquatic invertebrates, which are a critical food source for the numerous waterbird species that breed in the boreal. Invertebrates are of particular importance for the optimal growth and survival of waterbird chicks. However, observations of long-term change to boreal aquatic habitats and their invertebrate populations associated with a warming climate has been implicated in the declines of some boreal breeding waterbirds, such as the lesser scaup (*Aythya affinis*). Lesser scaup are known to feed extensively on amphipods, a freshwater crustacean; however, ducklings have been shown to have a diverse diet. Our goal was to use the naturally occurring heterogeneity of aquatic invertebrates across boreal lakes within the Yukon Flats National Wildlife Refuge in interior Alaska to better understand how changes in invertebrate prey resources might affect diet selection and growth in lesser scaup ducklings. First, we used a stable isotope approach to quantify the variation in the trophic niche within our population of ducklings. We found that as a population, lesser scaup ducklings consume a variety of aquatic insects, crustaceans and mollusks, and that variation in the population diet is largely attributable to variation in diet between birds from different lakes with different invertebrate communities. Second, we used the same habitat heterogeneity to examine how gradients of invertebrate abundance relate to the growth of ducklings. We observed that lesser scaup ducklings experienced reduced growth rates in lakes that had little to no amphipods. Taken together, these results suggest that while lesser

scaup ducklings are a flexible consumer that can adapt to changes in invertebrate populations, ducklings may face negative fitness repercussions when consuming prey other than amphipods.

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Chapter 1 General Introduction

This study examines the feeding ecology of lesser scaup (*Aythya affinis*) ducklings within the Yukon Flats, a large boreal wetland basin in interior Alaska. Lesser scaup are the most abundant diving duck in North America yet are considered a species of conservation concern under the North American Waterfowl Management Plan (USFWS 2011). The breeding population of scaup (lesser and greater [*Aythya* marila] combined) began declining in the 1980's and despite subsequent gains, the 2018 estimate of the scaup breeding population is 20% below the long-term average of 5 million and 37% below the management goal of 6.3 million birds (USFWS 2018). Although lesser and greater scaup are indistinguishable from one another during spring population surveys, lesser scaup (hereafter scaup) are believed to comprise 89% of the continental scaup population and hence are thought to be more severely declining and a greater conservation concern (Austin et al. 2006).

The northwest boreal forest of Canada and Alaska is the core breeding area for scaup (Austin et al. 2014). Globally, the boreal biome is a vast forested landscape interspersed with numerous lentic and lotic waterbodies, which may account for 80% of the earth's unfrozen freshwater (Schindler 1998). The high concentration of wetlands and the abundant aquatic invertebrate populations that they harbor make the boreal region an internationally important area for numerous waterbird species (Wells et al. 2011). Scaup ducklings, like other juvenile waterfowl rely on abundant aquatic invertebrates for optimal growth and survival (Cox et al. 1998). The Yukon Flats, the site of this study, is a large boreal wetland basin in interior Alaska. Over 800,000 pairs of ducks annually breed on the Yukon Flats, which supports the highest densities of breeding scaup in Alaska (USFWS 1987) likely because of the highly productive wetlands and high densities of invertebrates (Lewis et al. 2015).

While boreal regions in North America are under increasing pressure from resource development, much of the area is still considered pristine. However, recently observed changes related to a warming climate may affect critical breeding habitat for scaup. For example, in Alaskan boreal wetlands there is evidence that warmer temperatures and the associated increased evaporation and permafrost degradation have led to losses of wetland surface area (Riordan et al. 2006). This in turn has the potential to affect food web dynamics at multiple trophic scales. Indeed, several groups of aquatic invertebrates in Yukon Flats wetlands have experienced significant declines in abundance since the 1980's (Corcoran et al. 2009, Lewis et al. 2016). These long-term changes in ecosystem structure have the potential to reduce the total amount of high-quality brood rearing habitat in the region. Additionally, Drever et al. (2011) suggested that advancement of spring phenology associated with climate change has contributed to scaup declines by creating a temporal mismatch between scaup ducklings and their invertebrate prey. As such, examining the feeding ecology for scaup in boreal breeding wetlands has been identified as a research priority (Austin et al. 2014).

I addressed critical information gaps regarding scaup duckling feeding ecology in boreal wetlands by investigating the causes and consequences of dietary variation. I did so by taking advantage of the existing spatio-temporal habitat heterogeneity among Yukon Flats lakes. Scaup ducklings are known to feed extensively on amphipods (*Gammarus* and *Hyalella* spp.)(Bartonek and Murdy 1970, Sugden 1971, 1973, Gurney et al. 2017). Additionally, wetland use by scaup broods has been positively associated with the presence of amphipods (Fast et al. 2004, Lewis et al. 2015). However, scaup ducklings also feed on a wide variety of other invertebrates including aquatic insects, mollusks, and crustaceans (Bartonek and Murdy 1970). Recent work has demonstrated the patchy distribution of invertebrates within lakes across the same landscape.

Amphipods, for example, have the highest mean density among Yukon Flats wetlands, but are also the most variable and completely absent from some habitats (Lewis et al. 2015).

In my first chapter, I employ stable isotope techniques to investigate scaup duckling prey use. I aim to identify the factors that contribute to intra-population niche variation, both between and within wetlands with varying food resources. This work identifies the overall key diet items for scaup ducklings in boreal wetlands and quantifies the level of flexibility that ducklings have in their diet selection. Our second chapter examines the potential fitness consequences of such variability in food resources by measuring the growth of ducklings across the gradient of invertebrate abundance naturally occurring among Yukon Flats lakes. By understanding how existing habitat heterogeneity affects duckling diet selection we provide insight into how large-scale ecosystem changes related to a warming climate may affect scaup populations.

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Chapter 2 The Role of Habitat Heterogeneity in Intra-Population Niche Variation in a Boreal Waterbird Chick[1]

2.1 Abstract

Understanding the strength and causes of intra-population niche variation (IPNV) has important implications for wildlife conservation, yet they are rarely investigated. Populations of animals may be considered to be somewhere along a continuum of generalist to specialist consumers. However, the niche of sub-populations and individuals can deviate significantly from the population average. Here, we examined the IPNV of juvenile lesser scaup (*Aythya affinis*), a boreal breeding duck of conservation concern. The objectives of this study are to examine the degree of specialization and variation in diet of scaup ducklings across lakes with varying aquatic invertebrate prey community composition and densities. We used MixSIAR, a Bayesian-based stable isotope mixing model, to estimate the proportional contribution of three broad invertebrate groups [Predatory (Odonata larvae), Pelagic (Gastropoda, Corixidae and Conchostraca) and Benthic (Amphipoda and Chironomidae larvae)] to scaup duckling diet. Additionally, the hierarchical nature of MixSIAR allowed us to estimate the variation within and between lakes by modeling "Lake" and "Individual" as random effects. At the population level, scaup ducklings consumed significant proportions of all three prey groups with the highest proportion coming from the Pelagic group, followed by the Benthic group and then the Predatory group. "Lake" accounted for most of the variation in the population diet indicating that individuals within lakes had relatively similar diets compared to individuals from other lakes. Together, these findings suggest that scaup ducklings are generalist consumers with variable diets and that prey availability drives selection.

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2.2 Introduction

The niche as described by Hutchinson (1957) is a measure of a species resource use in space and time with the designation of specialist and generalist consumers being described by the relative width of their trophic niche. Ecologists and conservationists have often treated conspecifics as ecologically equivalent (Violle et al. 2012). This, despite the recognition that resource use can vary within a population (Van Valen 1965) such that apparently generalist species may in fact be comprised of relatively specialized individuals (Bolnick et al. 2007). This concept was formalized by Roughgarden (1972) and expanded upon by Bolnick et al. (2002) in which the total niche width (TNW) of a species or population can be partitioned into two components: the variation within (WIC) and between (BIC) individuals, such that TNW=WIC+BIC. Indeed, Intra-population niche variation (IPNV) has been documented across a broad array of taxa and is likely a common phenomenon (Bolnick et al. 2003, Araújo et al. 2008) with the potential for evolutionary and ecological consequences (Bolnick et al. 2011).

Diverging nutritional demands, foraging capabilities or preferences associated with sex, age class and distinct morphological phenotypes are factors that commonly lead to IPNV; however, diet may still vary between individuals within these groups (Bolnick et al. 2003, Araújo et al. 2011). Individual specialization (IS), as defined by Bolnick et al. (2003) refers to individual niche divergence from the population average not attributable to the above-mentioned criteria. Araújo et al. (2011) found that IS is commonplace, often strong and may be related to behavioral phenotypes, resource diversity/abundance and inter/intra-specific competition. However, the generality of IS and the factors that facilitate its occurrence and strength are yet unresolved and warrant further research among a variety of species (Araújo et al. 2011).

While IS, specifically refers to conspecifics with access to shared resources, animals generally inhabit heterogeneous landscapes with temporal and spatial gradients in resource abundance. Even though ecologists have long recognized the role of landscape heterogeneity in ecological community dynamics, conservationists and managers often use simplified models of homogenous landscapes when modeling population dynamics and conserving habitat (Wiens 1976, Pickett and Cadenasso 1995). However, habitat heterogeneity can influence IPNV across a broad array of taxa, habitats and scales with implications for conservation planning. Recent evidence comes from peregrine falcons (*Falco peregrimus)* breeding along a marine-terrestrial gradient in the arctic (L'Hérault et al. 2013), American alligators (*Aligator mississippiensis*) occupying freshwater lakes or estuarine habitats in the American southeast (Rosenblatt et al. 2015) and gray wolves (*canis lupus*) with varying access to marine subsidies in coastal British Columbia (Darimont et al. 2009).

While it may be intuitive that habitat heterogeneity results in IPNV, predicting how animals respond to gradients in the abundance of diet items is not always clear. Optimal foraging theory (OFT) predicts that animals will select the most profitable prey by making trade-offs between energetic value and handling time, and that individuals will switch to alternative prey when preferred items become scarce (Stephens and Krebs 1986). However, OFT assumes that individuals can adequately assess these trade-offs. Furthermore, the costs and benefits of different diet items vary depending on the phenotypic trait variation of the individual consumers (Araújo et al. 2011). As such, empirical evidence for prey switching in the face of variable prey densities is inconsistent (Prugh and Oksanen 2005).

Boreal lakes, which account for a significant portion of the earth's unfrozen freshwater, are an ideal system to examine the drivers of IPNV as they represent discrete patches of aquatic habitat

in a forested terrestrial matrix (Schindler 1998). These highly productive aquatic habitats harbor abundant aquatic invertebrate populations and in the absence of fish in many boreal lakes, waterbirds are the top invertebrate predator. Of particular importance are the invertebrate food resources necessary for the optimal growth and survival of waterbird chicks (Cox et al. 1998). As such, the boreal zone is a globally important breeding area for dozens of waterbird species (Wells et al. 2011). However, the abiotic and biotic characteristics of boreal wetlands can be highly variable resulting in heterogeneity in the community composition and total abundance of aquatic invertebrates, ultimately playing a strong role in habitat selection by waterbird broods (Heglund 1992, Sjöberg et al. 2000, Lewis 2015). Long running research in boreal lakes in southern Finland indicates that adequate invertebrate food resources are the limiting factor driving the occupancy of lakes by waterfowl broods. Moreover, they found that a significant number of lakes were unoccupied by broods as the food resources are unsuitable for rearing chicks (Sjöberg et al. 2000, Gunnarsson et al. 2004, Nummi et al. 2013). Similarly, in boreal wetlands in interior Alaska, waterbird species richness and occupancy by broods of several species were also predominantly explained by densities of invertebrates (Lewis et al. 2015a). Less apparent, however, is how such heterogeneity among occupied lakes affects diet selection of chicks. While decisions of habitat selection for duck broods are made by adult females, precocial ducklings are self-feeding. Thus, diet selection is being performed by a predator that may either be naïve in their assessment of the most profitable diet items or lack the ability to efficiently capture, digest and assimilate such items.

Here, we investigate the factors that contribute to the variation in diet for a population of a juvenile waterbird species, the lesser scaup (*Aythya affinis*), in the Yukon flats of Alaska. Lesser scaup (hereafter scaup) are an appropriate model species for testing hypotheses about the drivers

of IPNV. They are one of the most abundant diving ducks in North America (USFWS 2018), ducklings consume a variety of invertebrate prey (Bartonek and Murdy 1970, Sugden 1973, Gurney et al. 2017), and broods occupy discrete water bodies with spatial-temporal variations in invertebrate abundances (Heglund 1992, Lewis 2015, Gurney et al. 2017). Further, scaup are a species of management concern and changes to boreal lake surface area, limnology and aquatic foodwebs (Riordan et al. 2006, Corcoran et al. 2009, Roach et al. 2011, Lewis et al. 2015b, 2016) related to a warming climate have been implicated in population declines (Austin et al. 2006, 2014, Drever et al. 2011). Understanding how chicks respond to existing variation in invertebrate abundance may aid in predictions as to how ecosystem change will affect foraging and population dynamics.

Our objective was to quantify the IPNV of scaup ducklings across a heterogeneous landscape. We estimated diet using stable isotope techniques (Phillips 2001) and used hierarchical Bayesian mixing models to partition the population trophic niche (Semmens et al. 2009). Specifically, we aimed to determine 1) the relative width of the trophic niche of a population of scaup ducklings from the Yukon flats of Alaska, 2) the magnitude of niche variation within the population and the drivers of IPNV by 3) comparing the relative importance of individual specialization and habitat heterogeneity in structuring IPNV and 4) the role of invertebrate abundance in determining diet composition. We predict i) that at the population level, scaup ducklings will be relative generalists, consuming a wide range of invertebrate prey, ii) with considerable variation in their assimilated diet across the population, iii) while we predict that IS will be present in the form of variable diets among ducklings within lakes, we predict that habitat heterogeneity will lead to greater variation between lakes and years and iv) that the use of key invertebrate taxa will be positively related to their abundance.

2.3 Study Area

We conducted our work on the 8.6 million-acre Yukon Flats National Wildlife Refuge (YFNWR) located approximately 100 miles north of Fairbanks, Alaska. The Yukon Flats is a boreal wetland basin consisting of numerous shallow lakes and wetlands bisected by the Yukon River. We visited six study plots distributed across the refuge (Fig. 2-1). The plots were randomly selected as part of a study classifying wetland habitats and waterbird relationships in the 1980's (Heglund 1988, 1992) and were being resampled to assess decadal ecosystem changes (Lewis 2015). Upland habitat is typical of the boreal forest ecosystem and is dominated by black and white spruce (*Picea mariana, P. glauca*), Alaska birch (*Betula neoalaskana*), quaking aspen (*Populas tremuloides*), balsam poplar (*P. Balsamifera*) and willow (*Salix spp.*).

Our study involves 12 lakes ranging from 4 to 283 ha, a sub set of those that were concurrently being studied by Lewis (2015). They were typically shallow (< 2 meters) and eutrophic (median Total Phosphorous concentration=61µg/l). The vegetative zone of the lakes was dominated by emergent and submerged aquatic macrophytes including cattail (*Typha latifolial*), sedge (*Carex spp.*), bulrush (*Scirpus spp.*), pondweed (*Potamogeton spp.*), hornwort (*Ceratophyllum spp.*), water lilly (*Nuphar*) and watermilfoil (*Myriophyllum spp.*). The most abundant aquatic invertebrate taxa were Amphipods (*Gammarus lacustris, Hyalella azteca*), clam shrimp (Order: *Conchostraca*), Gastropods (Families: *Physidae spp., Planorbidae spp.*), midge larva (Order: *Diptera,* Family: *Chironomidae spp.*), water boatmen (Order: *Hemiptera,* Family: *Corixidae*), dragonfly and damselfly larva (Order: *Odonata*) and caddisfly larva (Order: *Trichoptera*) (Lewis 2015).

2.4 Methods

Sample Collection

We collected ducklings using shotguns from canoes under accordance with the Institutional Animal Care and Use Committee at the University of Alaska-Fairbanks during the summers of 2010-2012. We attempted to collect actively feeding ducklings although this was not always possible as broods would become alert and stop feeding as we approached. Generally, we collected one duckling per brood with a second duckling occasionally collected from creched broods. We assigned ducklings into age classes (5-9 day range) based on plumage characteristics (Gollop and Marshal 1954). Immediately upon collection, we dissected ducklings, removed and preserved the contents of their gastrointestinal tract in 100% ethanol. We removed a small piece of breast muscle from ducklings and preserved it in ethanol as well. In the laboratory, we identified stomach contents and counted mostly intact individuals. We calculated the dry mass for each individual invertebrate using a length-weight regression,

$$\ln DM = \ln a + b \ln L \qquad 2.1$$

(Benke et al. 1999). Where DM = dry mass (mg), L=length (mm) of specimen and a and b are constants derived from published length-weight regressions for the closest available taxon ((Benke et al. 1999, Miserendino 2001, Sabo et al. 2002, Gruner 2003, Baumgärtner and Rothhaupt 2003)Appendix).

Lake invertebrate samples were collected as part of a concurrent study by Lewis (2015) examining long-term ecosystem change. Invertebrates were collected with sweep nets and stored in ethanol (See Lewis et al. 2015a for a full methodology). In the laboratory, we identified invertebrates to the lowest practical taxonomic level, counted and measured individuals to the nearest mm. We estimated dry mass using Equation 2.1 as described above. Here we report invertebrate biomass as mg/sweep averaged for each lake and year during the brood rearing period. Large individual gastropods could grossly overestimate biomass available for ducklings. Therefore, we limited gastropod specimens to those that were $\leq$ 15mm, the maximum size we observed in gut contents.

We selected invertebrate taxa from these samples for SIA that were both common in lakes as well as in gut contents of our ducklings (Table 2-1). To account for spatial variation in baseline stable isotope signatures between lakes, we sampled aquatic invertebrates from the same lakes on which we collected ducklings. To account for intra-seasonal variation in isotope values we matched the timing of our invertebrate samples to the closest available date of our duckling collections. We attempted to account for inter-annual isotopic variation as well; however, time and budget constraints required us to pool invertebrate samples across years.

Stable Isotope Analysis

We freeze dried all samples to a constant mass. We triple rinsed invertebrates with a 2:1 chloroform:methanol solution to remove lipids as they are known to be depleted in C^{13} and can bias diet estimates if not accounted for (Post et al. 2007). Additionally, for snails we removed shells and treated the remaining tissue with hydrochloric acid (HCL) to remove any remaining bicarbonates, as they are not assimilated into the muscle of consumers. Depending on the size of

individual invertebrates and the number available, we either processed whole individuals or homogenized between 1 and 30 individuals using a mortar and pestle. We weighed 0.3-0.5 g of invertebrate and duckling tissue samples into tin capsules, which were analyzed for stable isotope ratios of Carbon and Nitrogen in a continuous flow isotope-ratio mass spectrometer (IRMS) by the Alaska Stable Isotope Facility. Isotope values are expressed in the standard δ notation in which $\delta^{13}C$ or $\delta^{15}N$ is the parts per thousand deviation (‰, per mil) from the standard materials of Pee Dee belemnite (PDB) limestone and atmospheric nitrogen respectively. δ= ([Rsample / Rstandard] - 1) X 1000, where R is the ratio of the heavy to light isotope of an element (^{13}C /^{12}C and $^{15}N/^{14}N$). Accuracy was determined by running replicates of the ASIF laboratory standard, Peptone.

Data Analyses

Before converting our stable isotope data to diet estimates using mixing models, we explored the drivers of variation in $\delta^{13}C$ and $\delta^{15}N$ for invertebrates and ducklings using general linear models. We used Akaike Information Criterion corrected for sample size (AIC_c) to determine the best fitting model (Burnham and Anderson 2002) from an a priori set of models. We used combinations of the explanatory variables of "Taxa", "Lake", "Year" and "Season (early or late)" for invertebrates and "Lake", "Age", "Year" and "Season" for ducklings. Due to known spatial variation in isotope values, we then explored general patterns of duckling and invertebrate $\delta^{13}C$ and $\delta^{15}N$ with Least-Square mean (LSM) estimates averaged across lakes. We used these analyses to guide our source inputs for our stable isotope mixing model (SIMM).

We used MixSIAR v 2.1.2 (Stock et al. 2018), a Bayesian based SIMM in the R statistical software, to estimate the proportional contribution of invertebrate prey to scaup duckling diet.

MixSIAR represents several advances in stable isotope mixing models (SIMMs): it allows the inclusion of covariates nested within a hierarchical structure allowing us to examine the diet of ducklings at the population, lake, and individual levels (Semmens et al. 2009). As a Bayesian SIMM, MixSIAR also incorporates prior information, such as gut contents, and accounts for uncertainty in prey isotope values and discrimination factors with uncertainty in the results taking the form of credible intervals (Parnell et al. 2013). Here we use uninformative priors due to the above-mentioned biases in gut content analysis. We used values from the literature to determine our discrimination factor, which is the characteristic change in the δ value for a given isotope ($\delta^{13}C$ and $\delta^{15}N$ here) as the elements are transferred from prey to consumer tissues (denoted as $\Delta^{13}C$ and $\Delta^{15}N$) (Mccutchan et al. 2003, Hornung and Foote 2008).

Model fitting was performed using Markov chain Monte Carlo (MCMC) sampling methods by running three parallel chains with an initial chain length of 300,000 iterations, after an initial burn-in of 200,000 and a thinned by 100. We used Deviance Information Criterion (DIC) to assess the relative fit of competing models containing combinations of our categorical covariates of interest (Lake, Year, and Individual as random effects) (Spiegelhalter et al. 2002). Convergence was assessed using the Gelman Rubin Diagnostic Test (Gelman et al. 2014). After identifying appropriate models, we estimated parameters from posterior probability distributions to infer the proportional contribution of prey groups to scaup duckling diet (Parnell et al. 2013). In the hierarchical structure of MixSIAR, the diet estimates for each level of population structure are drawn from the posterior distribution of the preceding level. For example, in our system, the mean for each lake is drawn from the population distribution with the mean for individuals drawn from their corresponding lakes.

To quantify the amount of variation in the population diet we measured the degree of niche overlap. Using the median values of diet estimates from the posterior distributions of our model outputs we calculated the proportional similarity index (PS_i). PS_i was originally developed to measure interspecific diet overlap (Schoener 1968, Feinsinger et al. 1981), adapted by Bolnick et al. (2002) to measure IS and can be used to measure niche overlap between any level (i.e. lakes) and the population diet. PS_i is calculated as

$$PS_i = 1 - 0.5 \, \Sigma_j \, \mathbf{I} \, p_{ij} - q_j \, \mathbf{I} \qquad 2.2$$

Where p_{ij} is the proportion of resource j in the diet of individual (or lake) i and q_j is the proportion of resource j in the population diet. Values for PS_i approach 1 as the proportional use of all diet items closely resembles that of the population and decreases towards 0 as the niche in question diverges from the population. To test our prediction that scaup duckling prey selection is related to invertebrate abundance we examined the relationships between diets, using the median values from SIMM estimates for each of the three diet groups, and invertebrate density or biomass. We used AIC model selection to compare the relative fit of models containing either the density or biomass of the invertebrate taxa which corresponds to each diet group.

2.5 Results

Duckling Collections

Over the course of three summers (2010-2012) we collected 103 scaup ducklings from 27 lakes. Here we limit our analysis to lakes with at least four ducklings collected, leaving us with 71

ducklings from 12 lakes. Each lake was sampled from 1-3 years for 24 "Lake" x "Year" combinations. Ducklings ranged in age from class 1C to 2C based on plumage class with a potential range of 14-42 days old based on the minimum and maximum ages of their respective classes. The mean (±SD) age of ducklings based on the midpoint of each subclass was 27 (±5) days. The date of duckling collections ranged from July 30 to September 4 with a mean (±SD) date of August 11 (±7 days).

Gut Content Analysis

Of the duckling stomach contents that we examined, 30 contained identifiable invertebrate food items with a total of 808 specimens from 13 different taxonomic orders observed (Table 1). Amphipods were the most abundant invertebrate in gut contents, with 367 (45.4%) specimens summed across all 30 ducklings. However, they were only found in 6 ducklings with 68% of all the amphipods being found in one duckling. Odonata were the most commonly occurring diet item, with 81 specimens found in 14 (47%) of duckling gut contents. While Odonata only represented 10% of the proportion of total invertebrates encountered, due to their relatively large size per specimen they accounted for over 45% of the estimated total biomass. Similar to their prevalence in gut contents, Amphipods and Odonata accounted for nearly 60% of the biomass of scaup diet items in lakes (39% and 19.6%, respectively). The remaining proportion of ingested invertebrates (Count and Biomass respectively) were Conchostraca (10%, 2.4%), Gastropods (9.3%, 11.1%), Corixids (5.4%, 4.8%), Chironomids (11.5%, 3.7%), Trichoptera (6.6%, 19.2%) and other taxa (1.7%, 1.1%) (Table 1). Of note is the high proportional biomass from Trichoptera, given their relative scarcity in lake samples (0.8% of biomass). Seeds were nearly ubiquitous in duckling gut contents. However, they were limited to the gizzards and given their slow rate of digestion, likely did not contribute significantly to the assimilated diet (Swanson and

Bartonek 1970). We presume that they may have been ingested either incidentally or as a substitute for grit as the lakes we studied had flocculent bottoms with thick organic layers.

Stable Isotope Analysis

Stable isotope ratios for duckling breast muscle and invertebrates were highly variable. For ducklings (n=71), $\delta^{13}C$ ranged from -35.1 ‰ to -14.7 ‰ and $\delta^{15}N$ ranged from 4.4 ‰ to 13.6 ‰. When explaining the $\delta^{13}C$ variation in duckling tissue, the top supported model from AIC model selection included Lake, Season and Age (ω_i =0.5). For $\delta^{15}N$, the top supported model included Lake and Year (ω_i =0.37). We focused our stable isotope sampling on six taxa that were common in gut contents and abundant in our study lakes (Table 1): Amphipods, Chironomids, Conchostraca, Corixids, Gastropods and Odonata (n=497). For invertebrates, $\delta^{13}C$ ranged from -34.4 ‰ to -10.2 ‰ and $\delta^{15}N$ ranged from –0.1 ‰ to 12.8 ‰. The top supported model for $\delta^{13}C$ variation in invertebrates included Lake, Taxa, Year and Day (ω_i =0.99). For $\delta^{15}N$, the top supported model included Lake, Taxa and Year (ω_i =0.35).

Least-squared mean estimates of invertebrate taxa $\delta^{13}C$ and $\delta^{15}N$ averaged over the levels of Lake, Year and Day showed substantial overlap among several taxa (Fig. 3). SIMMs are most effective when sources are isotopically distinct and such overlap necessitated post-hoc aggregation of invertebrates into prey groups for inclusion in the SIMM. We ran our mixing model with three source groups, based on functional feeding groups: Predators (Odonata), Benthic (Amphipod and Chironomid) and Pelagic (Conchostraca, Corixidae and Gastropoda).

Our top ranked model based on DIC contained only "Lake" as a random effect (ω_i =0.98 Table 2). The relative lack of support for models containing "Year" and/or "Individual" indicates that spatial heterogeneity is the most important factor contributing to trophic variation. As such, it is

appropriate to describe diet at this scale and we therefore base our remaining inferences using the model including only Lake as a random effect (Semmens et al. 2009). At the population level, scaup ducklings exhibited a generalist pattern with all three sources estimated to contribute considerable proportions of the diet. The highest proportion of the diet was from the Pelagic group with a median estimate of 62% (95% credible interval=29-88%). The remainder of the diet was attributed to the Benthic and Predator groups with median diet estimates of 23% (95% CI=5-52%) and 12% (95% CI=1-40%) respectively. (Fig. 4). Estimates for the relative contributions of each source to consumer tissues varied by lake. Among the 12 lakes measured, the median proportional estimates ranged from 5-76% for the benthic group, 14-90% for the pelagic group and 2-53% for the predator group. (Fig. 5). The niche overlap (PSi) between the lake specific and the population level diet ranged from 45-98% with the average level of overlap being 70%.

Support for the positive influence of invertebrate abundance (biomass or density) on the proportional use of the associated diet groups was lacking. The top supported model explaining the proportional use of the Benthic group was the intercept model (ω_i=0.4) indicating little support that the use of this diet group is driven by the abundance of Amphipods (biomass: ω_i=0.12, β=-0.00003, 95% CI: -0.002 – 0.0019; density: ω_i=0.12, β=-0.0002, 95% CI: 0.0008 – -0.0014) or Dipterans (biomass: ω_i=0.15, β=-0.0063, 95% CI: -0.0106 – 0.0232; density: ω_i=0.18, β=-0.0023, 95% CI: -0.0026 – 0.0072). For the Pelagic group, the top two models indicate a negative relationship with the abundance of Hemipterans (biomass: ω_i=0.49, β=-0.0131, 95% CI: -0.0221 – -0.0041; density: ω_i=0.25, β=-0.0204, 95% CI: -0.0363 – -0.0045). There was no support for the effect of the abundance of Conchostraca (biomass: ω_i=0.04, β=-0.0145, 95% CI: -0.0037 – 0.0327; density: ω_i=0.04, β=-0.0063, 95% CI: -0.0019 – 0.0145) or Gastropods (biomass: ω_i=0.01, β=0.0002, 95% CI: -0.001 – 0.0014; density: ω_i=0.09, β=-0.0039, 95% CI: -

0.0078 – 0.00002). The use of the Predator group was positively influenced by the abundance of Odonata (biomass: ω_i=0.59, β=0.0075, 95% CI: 0.0028 – 0.0122; density: ω_i=0.39, β=-0.0196, 95% CI: 0.0069 – 0.0323).

2.6 Discussion

Our investigation of the feeding ecology of scaup ducklings across a large, heterogeneous boreal wetland basin has advanced our knowledge about the factors that lead to niche variation, with potential implications for understanding how scaup may respond to a changing boreal environment. Evidence from gut contents and SIMMs supported our prediction that scaup ducklings on the Yukon Flats are generalist consumers with a wide trophic niche that rely on a variety of aquatic invertebrates. Within our hierarchical SIMM, "Lake" was the most important factor explaining dietary variation, supporting our prediction that intra-population niche variation is present and driven by spatial heterogeneity in resources. Less support for "Year" in our models suggested that inter-annual variation in resources may have had a modest, but lower effect on niche variation. Despite our prediction of a moderate effect of "Individual" in our models, we found no evidence of IS within any of our study lakes. Diet of ducklings within lakes was much more similar than the diet of ducklings from other lakes, suggesting that scaup are flexible in their response to variations in prey abundance. Perhaps, such adaptability bodes well for scaup as aquatic foodwebs in boreal wetlands continue to change.

Population Level Diet

Scaup ducklings in our study consumed a variety of invertebrate prey as confirmed by gut contents and SIA, supporting our prediction of dietary generalization at the population level. Gut content samples contained invertebrates from 11 different taxonomic Orders, seven of which

were found relatively frequently. Similarly, our SIMM results suggest a wide trophic niche for this population in which all three source groups contributed significantly to the diet (Figure 4).

The designation between generalists and specialists is often poorly defined and may be arbitrary (i.e. >50% of diet from one source). Here our aim was to provide a qualitative assessment of the level of dietary specialization for the population. The Pelagic group represented the highest proportional contribution to the population diet (median estimate of 62% and 95% CI: 29-88%). The remaining proportion of diet was from the Benthic group (median: 23%, 95% CI: 5-52%) and the Predator group (median: 12%, 95% CI: 1-40%). While the Pelagic group may have contributed most of the total diet, we do not feel this indicates specialization. We were unable to partition the proportional contribution of the taxa that were aggregated in the Pelagic and Benthic groups. This is a common problem when reconstructing diet using stable isotopes and limited our ability to measure niche width (Parnell et al. 2010). We presume that Conchostraca and Amphipods were the primary contributors to the Pelagic and Benthic groups respectively, given their previously found importance in studies of scaup duckling diet (Bartonek and Murdy 1970, Gurney et al. 2017) and their relatively high occurrence in our gut contents. Their large size and conspicuous nature likely make Conchostraca and Amphipods profitable diet items for scaup ducklings. However, Gastropods and Corixids also likely contributed to the Pelagic diet as they were relatively common in gut content samples. Chironomids likely contributed to the Benthic group diet as well, albeit, to a lesser extent than Amphipods given their relatively lower occurrence in gut contents. Given the wide range of putative diet items, limiting our stable isotope approach to only three source groups likely underestimated niche width and its variation. Even so, our finding of a diverse diet comprised of crustaceans, insects and mollusks indicates a high level of generalization, which confirms the findings of Gurney et al. (2017).

Even if the Benthic group was comprised entirely of Amphipods, the proportional contribution from this group was lower than might be expected considering the previously indicated importance of Amphipods in studies of duckling diet and brood habitat selection (Bartonek and Murdy 1970, Sugden 1973, Lindeman and Clark 1999, Fast et al. 2004, Gurney et al. 2017). Indeed, concurrent research on our study area has shown that Amphipod density is an important factor in explaining scaup brood occupancy (Lewis et al. 2015a). Several possible explanations exist as to why Amphipods were not a higher proportion of the diet. Despite high densities of Amphipods on our study lakes, it is possible that observed population declines (Corcoran et al. 2009, Lewis et al. 2016) may have crossed a density threshold requiring scaup ducklings to use alternative prey. Alternatively, ontogenetic diet shifts by ducklings may be responsible. Although ducklings are capable of diving bouts within the first few days of life, their capacity to feed effectively on benthic invertebrates appears to increase with age (Bartonek and Murdy 1970, Sugden 1973). This is perhaps well timed with the seasonal increase in Amphipod biomass observed in boreal wetlands (Gurney et al. 2017). While most of the ducklings in our study fell within the age classes that are capable of benthic feeding, our use of breast muscle in SIA with its relatively long turnover time may have muted the signal from any diet shifts (Hobson and Clark 1992). Therefore, our results indicating higher use of the Pelagic group may be in accordance with the observations by Bartonek and Murdy (1970) that the diet of scaup ducklings shifts from one dominated by Conchostraca in the younger age classes (IA-IIA) to that of Amphipods in the older classes (IIA-III).

Patterns of Niche Variation

To determine the relative strength of drivers of IPNV we used a model selection criteria (DIC) to evaluate the support for the inclusion of covariates in our mixing models (Semmens et al. 2009).

As we predicted, most of the variation in scaup duckling diet on the Yukon Flats was driven by the variation between lakes as indicated by the top model in our set containing only "Lake" as a covariate (DIC=4029.5, ω_i=0.98). Presumably, this was a result of the spatial variation in the composition and abundances of their invertebrate prey that we observed. Conversely, despite the inter-annual variation of invertebrate abundance we observed and the apparent commonality of IS found in numerous taxa by Bolnick et al. (2003) there was very little support for variation attributable to "Year" and/or "Individual" as indicated by the low weight of the second highest ranked model which contained three hierarchical nested levels, "Lake", "Year" and "Individual" (DIC=4037.7, ω_i=0.02). Although, there was very little support for this model we can cautiously infer the relative contributions of annual and individual variation to IPNV by comparing the variance parameters of the three factors (Semmens et al. 2009). The median values for the posterior distributions of diet variance were similar for "Lake" and "Year" ($\hat{\sigma}_{lake}$=0.869, 95% CI:0.07-3.34 and $\hat{\sigma}_{year}$=1.083, 95% CI:0.244-2.712 respectively), however, the variance from "Individual" was several fold lower ($\hat{\sigma}_{ind}$=0.233, 95% CI:0.012-0.977) indicating that along with spatial variation, annual variation may possibly contribute to IPNV, yet variation among co-occurring individuals is minimal. Similar to the findings of Gurney et al. (2017), our results suggest that scaup ducklings can adapt their foraging strategies when faced with variations in their prey base.

While we found that spatial heterogeneity was the primary driver of IPNV, the average level of niche overlap between lakes and the population level was high (PSi=70%). Much like our inability to accurately measure niche width due to the aggregation of invertebrates, our measure of niche overlap may be biased. PSi may be overestimated if the overlap associated with a prey group is due to the use of different invertebrate taxa. Furthermore, we limited our analysis to

lakes in which we were able to collect four or more ducklings. These lakes tended to have multiple broods and were presumably higher quality habitat with similar invertebrate communities. Indeed, the variation in invertebrate abundances on the 12 lakes we studied was less than that measured on a larger set of lakes within our study area that were occupied by scaup broods (Lewis et al. 2015a). We might expect to see more dietary variation between lakes (lower PSi value) when including lakes with lower occupancy rates. Even so, we feel we were able to document considerable variation between lakes with median estimates ranging from 5-75% for the Benthic group, 15-90% for the Pelagic group and 2-46% for the Predator group. (Fig. 5).

We predicted that birds would consume prey in relative proportion to their abundance. Evidence for an effect of invertebrate abundance on the proportional contribution of the associated diet source was generally weak. The abundance of Odonata (biomass and density) were the only invertebrate factors which had a positive and significant (95% CI which did not encompass zero) effect on the proportional use of that prey group. Even so, the relationship was weak. The only other significant relationship was a negative one between Hemiptera abundance (biomass and density) and the proportional use of the Pelagic diet group. Particularly surprising was the lack of a positive relationship between the abundance of Amphipods and the proportion of the Benthic group in the diet given the previously documented importance of amphipods.

There are several reasons why invertebrate abundance may have been a poor predictor of scaup duckling diet. First, our measure of prey abundance may not reflect actual prey availability for scaup ducklings. As previously discussed, the age-related diet shifts and the inability of younger ducklings to feed in the benthos could mean that we sampled invertebrates that were unavailable to ducklings. Second, despite high prey densities ducklings may not be able to feed effectively on invertebrates concealed in dense submerged aquatic vegetation. Third, while one of our main

objectives was to investigate the effects of habitat heterogeneity across the landscape regarding variation in prey abundance among lakes, we did not consider the heterogeneous distribution of invertebrates within lakes. Micro habitats associated with vegetation complexity within lakes affects the distribution of aquatic invertebrates (Rennie and Jackson 2005) and using invertebrate densities averaged over a lake may obscure such patchiness. Predation risk or competitive exclusion may have relegated some broods to lower quality habitats with lakes. However, the lack of IS within lakes suggests that broods were not excluded from high density invertebrate patches by dominant conspecifics. Alternatively, invertebrate densities in our lakes may have been high enough that duckling prey selection was independent of abundance and was instead based on other measures of profitability such as capture efficiency, digestibility or micro/macro nutrient composition (Stephens and Krebs 1986).

Future Directions

To increase the utility of investigations of trophic interactions in boreal wetlands we suggest that researchers take steps to further refine diet estimates. More than two biotracers can be incorporated into the MixSIAR platform which could increase the resolution of mixing models (Stock et al. 2018). The addition of sulfur isotopes and even fatty acids may prove useful (Mccutchan et al. 2003, Wang et al. 2007). NexGen sequencing is a promising new research tool and would provide even more taxonomic resolution (Pompanon et al. 2012).

We suggest that with the hierarchal nature of MixSIAR we can expand our investigation of IPNV in scaup ducklings to include populations from other core breeding areas. Such that the population level diet would then encompass scaup breeding in the western boreal forest, which could be partitioned into regions such as the Yukon Flats of Alaska (this study) and breeding

areas in the Northwest Territories and Alberta Canada (Gurney et al. 2017). As demonstrated here, diet could then be further partitioned into lakes within regions and individuals within lakes. Simultaneously comparing the prey abundance and the demographic rates between regions may further our understanding of both the causes and consequences of niche variation.

Summary

Reporting diet at only the population level provides a narrow perspective of a species trophic niche (Bolnick et al. 2003). As such, our objective here was to examine the tropic niche of scaup ducklings, the patterns of variation in the population niche and the ecological causes of such variation. Our results showed that the diet of scaup ducklings varies between lakes, and to a lesser extent between years within lakes. Diet among individuals is more similar within lakes than between lakes, suggesting that prey availability is the primary driver of IPNV. Scaup ducklings from the Yukon flats appear to be able to adapt to variable invertebrate prey communities and densities by having a flexible diet. The fact that diet does not directly track the abundance of any invertebrate suggests that ducklings were not food limited in our study lakes. As a warming climate and development from resource extraction continue to alter boreal aquatic foodwebs it is uncertain if these patterns will persist. However, given that scaup are not dependent on any one prey type is encouraging as it potentially indicates a resilience to changing conditions. We agree with the recommendation of others that protecting boreal lakes with high amphipod densities should be a priority for scaup conservation. However, we do suggest that lakes without Amphipods can be important brood rearing habitat if they contain high densities of alternative prey such as Conchostraca. However, the fitness consequences of associated with variable diets would ultimately need to be determined.

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2.9 Figures

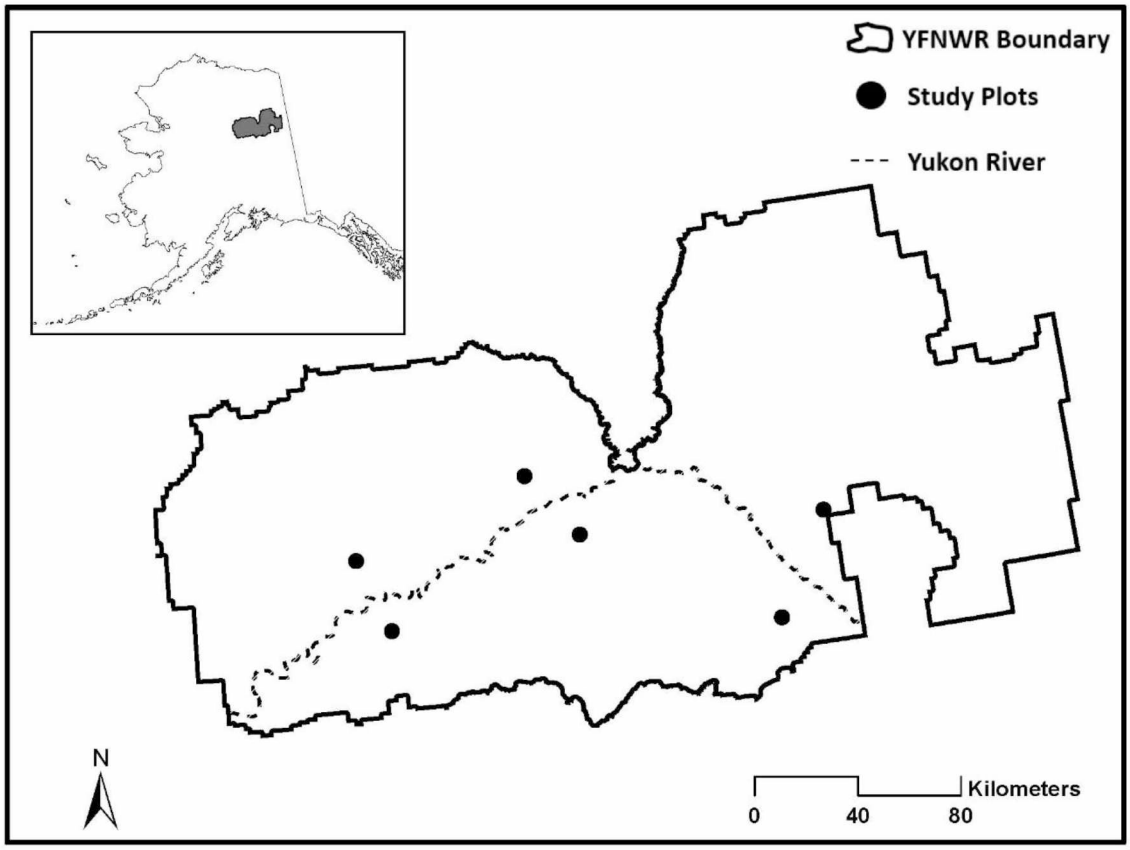

Figure 2-1. Map of the Yukon Flats National Wildlife Refuge study area with the six plots depicted by the black circles. The Yukon River, depicted by a dashed line, bisects the study area with three plots to the north and three plots to the south. The general location of the Yukon Flats National Wildlife Refuge within Alaska is depicted in the inset.

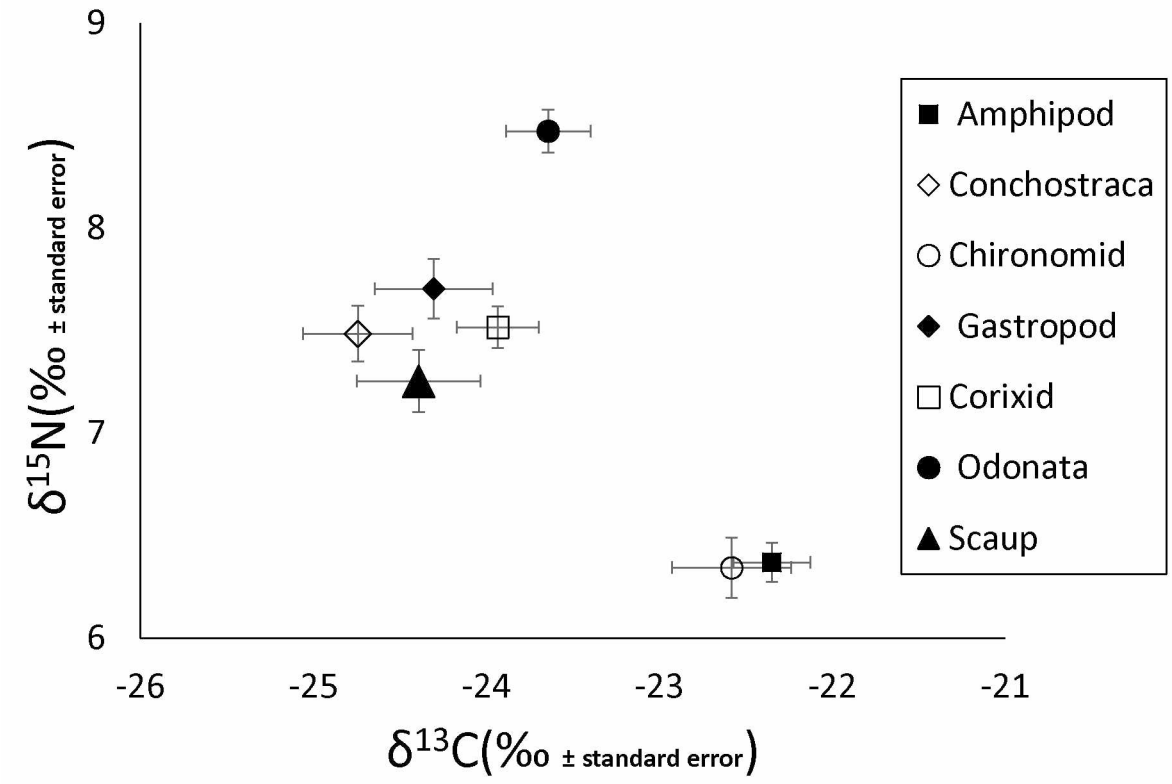

Figure 2-2. Least-squared mean estimates of Isotope values ($\delta^{13}C$, $\delta^{15}N$) for lesser scaup duckling breast muscle and putative aquatic invertebrate diet items collected from 12 lakes over three years. To account for spatial-temporal variation in isotope values, we averaged over the levels of lake, year and day to generalize trophic patterns in boreal aquatic foodwebs and inform our stable isotope mixing models. Invertebrate values include an isotopic discrimination factor to account for trophic enrichment.

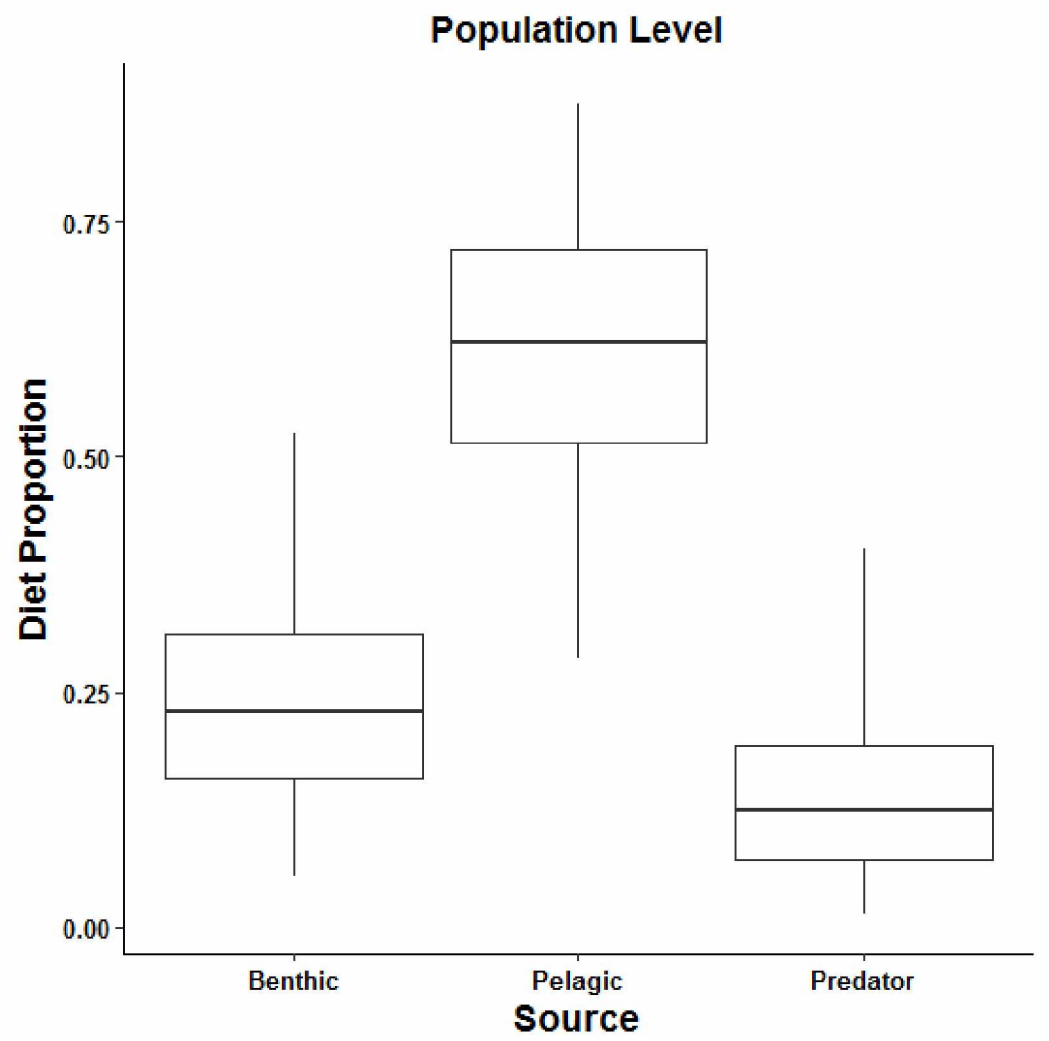

Figure 2-3. Posterior probability distributions of the proportional contribution of three invertebrate prey sources (Benthic, Pelagic and Predator) to scaup duckling diet at the population level across 12 lakes within the Yukon Flats National Wildlife Refuge. Values were derived from the model with the lowest DIC value. Middle bars=median estimates, boxes=50% credible intervals, whiskers=95% credible intervals.

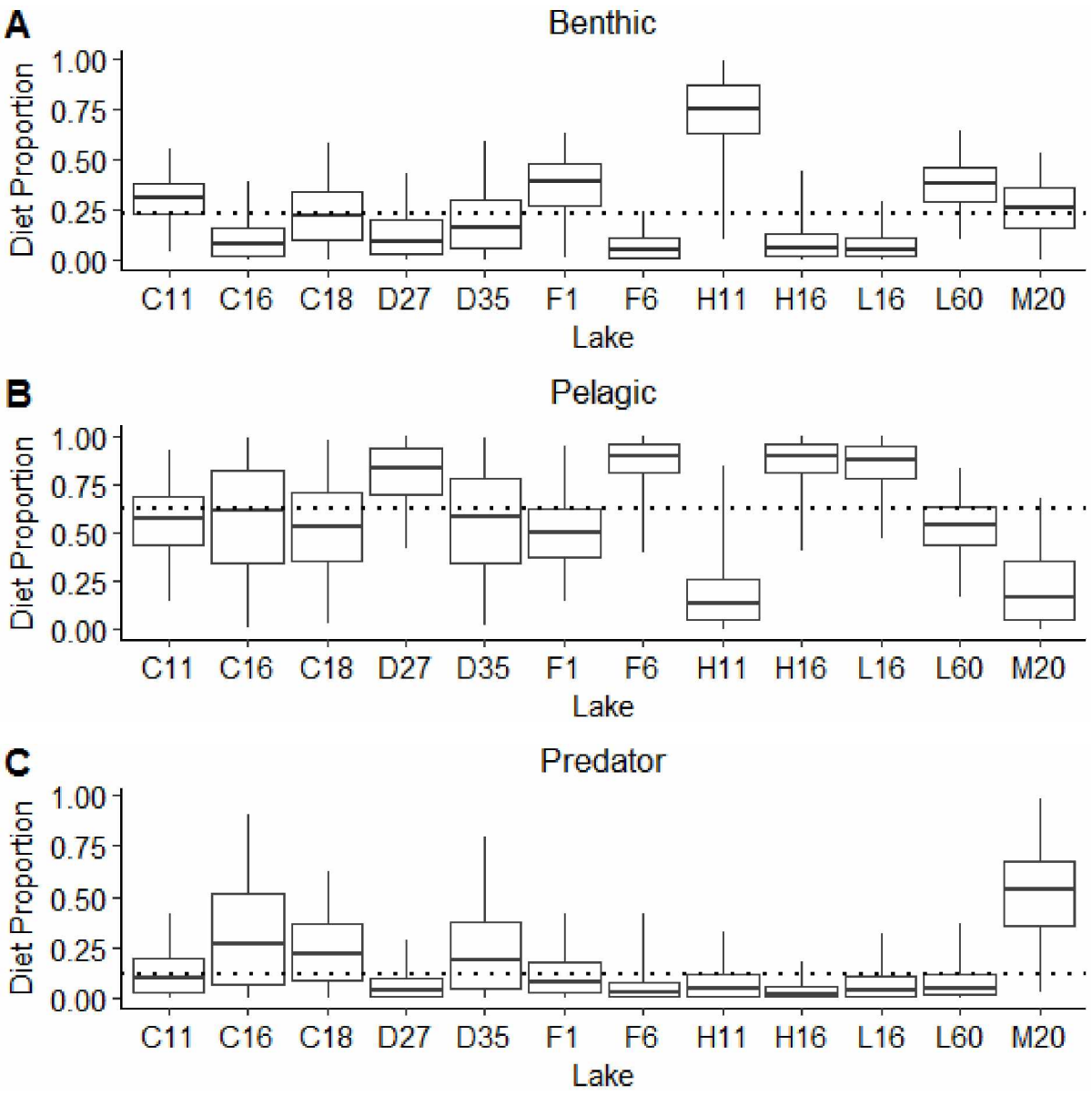

Figure 2-4. Lake specific posterior probability distributions of the proportional contribution of three invertebrate prey sources (A-C) to scaup duckling diet. Middle bars=median estimates, boxes=50% credible intervals, whiskers=95% credible intervals. Horizontal dotted line depicts the population level median across all 12 lakes.

2.10 Tables

Table 2-1. Invertebrate abundance in the gut contents of 30 scaup ducklings and 12 boreal lakes sampled over three years from which ducklings were collected. Invertebrate counts and biomass from gut contents are summed across all ducklings. Lake prey abundance (mean biomass and percent) is only reported for taxa which was documented in gut contents. Invertebrate biomass was estimated using length-mass regressions. Results were used to guide the inclusion of sources in stable isotope analysis.

Diet Item[a]	Duckling Gut Contents					Lake Prey Abundance	
	Specimens Counted		Biomass		Frequency of Occurrence n=30 ducklings	Mean (±SD) Lake Biomass (mg/sweep)	Percent (%)
	Total	Percent (%) of Total	Total (mg)	Percent (%) of Total			
Amphipoda	367	45.4	327.5	12.3	6	25.7 (33.7)	39
Chironomidae	93	11.5	98.9[b]	3.7	7	2.0 (4.0)	3
Odonata	81	10	1209	45.4	14	12.9 (10.5)	19.6
Conchostraca	80	9.9	62.88	2.4	11	3.3 (4.7)	5
Gastropoda	75	9.3	296.8	11.1	6	8.6 (8.2)	13.1
Trichoptera	53	6.6	511.9	19.2	7	0.5 (0.7)	0.8
Corixidae	44	5.4	128[b]	4.8	4	4.9 (8.3)	7.4
Oligochaete	9	1.1	0.05	tr[c]	6	tr[c]	tr[c]
Coleoptera	2	0.2	12.52	0.5	2	7.1 (8.7)	10.8
Hymenoptera	1	0.1	14.36	0.5	1	0[e]	0[e]
Ephemeroptera	1	0.1	3.58	0.1	1	0.5 (1.2)	0.8
Cladocera	1	0.1	0.01	tr[c]	1	NA[d]	NA[d]
Ostracoda	1	0.1	0.01	tr[c]	1	0.4 (1.0)	0.6

[a]Invertebrate diet items are arranged in decreasing order of total specimens counted in gut contents. [b]Lake biomass estimates for Chironomidae and Corixidae are based on the estimates for the Orders Diptera and Hemiptera respectively. [c]tr=trace (<0.01). [d]Lake biomass estimates for Cladocera and other zooplankton were not determined. [e]Hymenoptera were not encountered in lake sampling.

Table 2-2. Variation in scaup duckling diet is primarily driven by differences between lakes with varying food resources. Ranking for alternative Bayesian stable isotope mixing models is based on Deviance Information Criteria (DIC) and model weight (w_i)

Model Covariates	**DIC**	**ΔDIC**	w_i
Lake	4029.47	0	0.98
Lake(Year)+Individual	4037.69	8.21	0.02
Lake(Year)	4039.46	9.99	0
Lake+Age	4046.66	17.19	0
Lake+Individual	4058.99	29.52	0

Chapter 3 Growth of Juvenile Lesser Scaup Across a Gradient of Prey Abundance in a Boreal Wetland Basin[1]

3.1 Abstract

Boreal lakes and wetlands harbor abundant invertebrate populations, which serve as an important food source for numerous breeding waterbird species. The relationship between invertebrate abundance and the growth and survival of ducklings is well documented and long-term changes to boreal aquatic habitats and their associated invertebrate populations has been implicated in the decline of one such waterbird, the lesser scaup (*Aythya affinis*). Previous work has shown that lesser scaup ducklings have a diverse diet that may be able to compensate for reductions in any one diet item. We used the naturally occurring habitat heterogeneity across lakes within the Yukon Flats National Wildlife Refuge to examine how gradients in the biomass of invertebrates commonly consumed by lesser scaup ducklings impact growth. We found that amphipods were the only invertebrate which had a significant impact on duckling growth. Ducklings reared on lakes with low amphipod biomass were significantly lighter than those reared on lakes with even moderate amphipod biomass.

3.2 Introduction

Juvenile waterfowl have high growth rates which require abundant and high quality food sources (Sedinger 1992). During the brood period, ducklings are particularly reliant on protein rich aquatic macroinvertebrates (hereafter invertebrates) as a food source, with the relationship between invertebrate abundance and duckling growth being well documented (Street 1978, Cox et al. 1998). Duckling growth has been directly linked to the total number of invertebrates as well as habitat factors that act as proxies for invertebrate abundance including wetland nutrient status

[1]To be submitted for publication to The Auk as DuBour, A. J., M. S. Lindberg, K. E. B. Gurney and T. L. Lewis. 2019. Growth of juvenile lesser scaup across a gradient of prey abundance in a boreal wetland basin.

(Nummi et al. 2000, Sjöberg et al. 2000), degree of acidification (DesGranges and Hunter 1987, Rattner et al. 1987), insecticide treatment (Hunter et al. 1984), fish presence (DesGranges and Rodrigue 1986) and habitat type (Flint et al. 2006).

Fitness and survival of ducklings are in turn strongly influenced by growth rates. Ducklings typically experience low survival rates during the brood period primarily due to predation and inclement weather, with most mortality occurring during the first ten days of life (Walker and Lindberg 2005, Corcoran et al. 2007). However, slow growth rates exacerbate these sources of mortality (Cox et al. 1998). Nutritionally stressed ducklings may be weak and unable to evade predators and thermoregulate properly. Furthermore, in poor quality habitats ducklings spend more time searching for food, possibly at the cost of predator vigilance or brood care during cold rainy weather. For instance, Gunnarsson et al. (2004) observed higher mortality rates of mallard ducklings (*Anas platyrhynchos*) during inclement weather, but only for those reared on food-poor ponds.

Beyond brood period survival, ducklings with slower growth rates achieve a relatively smaller body size at fledging which may impact long-term survival and lifetime reproductive success (Haramis et al. 1986, Sedinger 1992). Smaller individuals may be at a disadvantage in competing for limited food resources on wintering grounds which could lead to a higher mortality rate (Raveling 1966). Lifetime reproductive success is lower for smaller individuals as their first breeding attempts tend to occur later in life (Cooke et al. 1984) and may lay smaller clutches (Ankney and Macinnes 1978, Dunn and Macinnes 1987). Furthermore, the impact of poor growth may carry over to subsequent generations (Sedinger 1992). Smaller females may provide inadequate brood care for their offspring. For example, relatively late hatched juvenile lesser scaup experienced lower survival when reared by lighter hens (Gurney et al. 2012).

Here we investigate the role of food abundance on the growth of juvenile lesser scaup (*Aythya affinis*) in boreal forest lakes of Alaska. Lesser scaup are the most abundant diving duck in North America yet are considered a species of conservation concern under the North American Waterfowl Management Plan. The breeding population of scaup (lesser and greater [*Aythya* marila] combined) began declining in the 1980's. Although the two species are indistinguishable during breeding pair population surveys, lesser scaup (hereafter scaup) are believed to comprise 89% of the continental scaup population and are thought to be more severely declining and therefore a greater conservation concern. The 2018 estimate of the scaup breeding population is 20% below the long-term average of 5 million and 37% below the management goal of 6.3 million birds (USFWS 2018). Several non-mutually exclusive hypotheses have been advanced to explain scaup declines with habitat conditions and food resources for ducklings on boreal breeding grounds being identified as one research priority (Austin et al. 2006).

While it follows that reduced growth rates of scaup ducklings associated with inadequate food sources have the potential to affect individual fitness and population dynamics, the western boreal forest is relatively pristine and contains highly productive aquatic habitats (Zoltai et al. 1988). However, large-scale ecosystem change associated with a warming climate may be affecting habitat quality and contributing to scaup population declines. For instance, (Drever et al. 2011) proposed that in years with early springs, the life-cycle timing of invertebrates advances and creates a temporal trophic mismatch between prey availability and scaup duckling demand (sensu Visser et al. 1998). Perhaps of more consequence; however, is the decline in boreal lake surface area since the 1950s (Riordan et al. 2006) and changes in aquatic food webs observed in Alaskan boreal lakes since the 1980s (Corcoran et al. 2009, Lewis et al. 2016). While some invertebrate populations have increased, populations of several invertebrate groups

have decreased significantly. Changes in the aquatic foodweb dynamics may have the overall impact of limiting the amount of high-quality brood-rearing habitat for scaup.

Amphipods (*Gammarus* and *Hyalella* spp.) have routinely been cited as an important prey for scaup. While a variety of insects, mollusks and crustaceans are consumed by ducklings, Amphipods are a common diet item (Bartonek and Murdy 1970, Sugden 1973, Gurney et al. 2017) and their abundance is an important predictor of brood habitat use (Lindeman and Clark 1999, Fast et al. 2004). Indeed, previous work indicated that Amphipod density was the most important factor explaining scaup brood occupancy of lakes in the Yukon Flats of Alaska (Lewis et al. 2015). However, invertebrate abundance, particularly Amphipods, was found to be highly variable in these lakes. While Amphipods reached the highest maximum densities compared to other invertebrates, they had the patchiest distribution and were completely absent from the bottom quartile of lakes (Lewis et al. 2015). Such heterogeneity appears to be the primary driver of diet variation for scaup ducklings (Gurney et al. 2017, DuBour 2019). Therefore, while Amphipods are likely an important diet item for scaup ducklings, it is unclear how the growth of such an adaptable consumer will respond to variations in their prey.

For scaup, general patterns of duckling growth have been investigated in captivity (Sugden and Harris 1972, Lightbody and Ankney 1984), however, investigations of growth in relation to natural food resources are limited. The objective of this study is to understand the role of variable food abundance in the growth of scaup ducklings. We did so by measuring the size-adjusted body mass of scaup ducklings across a spatio-temporal gradient of invertebrate abundance. To our knowledge, our study is the first examination of scaup duckling growth in relation to heterogeneous food resources in the wild. By taking advantage of the natural variation in habitat composition, we aim to highlight a factor that may contribute to scaup population

declines in the face of potential ecosystem change in boreal lakes. Given the reliance on invertebrates and limited time available to grow and fledge prior to migration, we predicted that scaup duckling growth would be positively related to overall invertebrate abundance**.** However, while scaup ducklings have a diverse diet, Amphipods appear to be an important food source. Therefore, we expected that Amphipod abundance would have an inordinate impact on duckling growth.

3.3 Study Area

We conducted our investigation within the Yukon Flats, a large boreal wetland basin consisting of numerous shallow lakes and wetlands bisected by the Yukon River. The Yukon Flats is almost completely encompassed by the 8.6 million-acre Yukon Flats National Wildlife Refuge (YFNWR) located approximately 100 miles north of Fairbanks, Alaska. The upland habitat of the Yukon Flats is typical of the boreal forest ecosystem and is dominated by black and white spruce (*Picea mariana, P. glauca*), Alaska birch (*Betula neoalaskana*), quaking aspen (*Populus tremuloides*), balsam poplar (*P. balsamifera*) and willow (*Salix spp.*) Lakes are typically shallow (< 2 meters) and eutrophic or hypereutrophic (median Total Phosphorous concentration=61µg/l). The vegetative zone of lakes is dominated by emergent and submerged aquatic macrophytes including cattail (*Typha latifolial*), sedge (*Carex spp.*), bulrush (*Scirpus spp.*), pondweed (*Potamogeton spp.*), hornwort (*Ceratophyllum spp.*), water lily (*Nuphar*) and watermilfoil (*Myriophyllum spp.*). The most abundant aquatic invertebrate taxa are Amphipods, clam shrimp (*Conchostraca*), snails (*Physidae, Planorbidae*), Chironomid midge larva (*Chironomidae spp.*), water boatmen (*Corixidae*), dragonfly and damselfly larva (*Odonata*) and caddisfly larva (*Trichoptera*) (Lewis 2015).

For this study we visited a subset of lakes originally established by Heglund (1988, 1992) as part of a study of waterbirds and their habitats in the 1980s, and concurrently studied by Lewis (2015) to assess decadal ecosystem changes. We sampled 27 lakes ranging from 0.2 to 283.2 ha within six study plots distributed across the refuge (Fig 3-1.).

3.4 Methods

Sample Collection

During the summers of 2010-2012 we collected ducklings using shotguns from canoes in accordance with the Institutional Animal Care and Use Committee at the University of Alaska-Fairbanks. Generally, we collected one duckling per brood with a second duckling occasionally collected from creched broods. We assigned ducklings into age classes (5 to 9-day range) based on plumage characteristics (Gollop and Marshal 1954). Immediately upon collection, we blotted ducklings with a dry cloth to remove any residual water and weighed carcasses with an electronic scale (± 0.1g). We then used calipers to take morphological measurements including culmen, head length, wing chord, tarsus, body length and length of the erupting ninth primary (±0.1mm). Carcasses were kept in cool storage in the field. Upon return from the field site all carcasses were frozen and stored at the University of Alaska Fairbanks. To corroborate the field measurements, all ducklings were re-measured by the investigator after the final year of sample collection. This occurred on a single occasion in a laboratory setting to ensure consistent measurement technique. Mass was not re-assessed, as tissue samples had been removed from the birds for separate analyses (DuBour 2019) and mass would not have been comparable to field results.

Invertebrate samples were collected as part of a concurrent study by Lewis (2015) examining long-term ecosystem change. Specimens were collected by pulling a D-frame net horizontally

through the water column for one meter just below the surface. Transects were randomly located around the lake's perimeter and ran perpendicular to the shore. Transects consisted of one to three sweeps, with one sweep per vegetation type encountered. Therefore, the number of samples taken per lake sampling event depended on lake size and the variety of vegetation types represented and ranged from 4 to 43 (See Lewis et al. 2015 for a full methodology). Invertebrate samples were stored in ethanol (90%) in the field and transported back to the laboratory.

In the laboratory we identified invertebrates to the lowest practical taxonomic level, counted and measured individuals to the nearest mm. We calculated the dry mass for each individual invertebrate using a length-weight regression,

$$\ln DM = \ln a + b \ln L \qquad 3.1$$

(Benke et al. 1999). Where DM= dry mass (mg), L=length (mm) of specimen and a and b are constants derived from published length-weight regressions for the closest available taxon ((Benke et al. 1999, Miserendino 2001, Sabo et al. 2002, Gruner 2003, Baumgärtner and Rothhaupt 2003)Appendix). Based on our previous observations of scaup duckling food habits we concluded that large individual gastropods could grossly overestimate available biomass. Therefore, we limited gastropod specimens to those that were $\leq$ 15mm, the maximum size we previously observed in gut contents (DuBour 2019). For each sweep sample we summed the dry mass of all the individuals for each taxon. Here we report invertebrate biomass as the average mg/sweep. In determining biomass, we limited our samples to those that corresponded to the

scaup brood rearing period, approximately from the last week of June to mid-August (personal observation). For most lake and year combinations (77%), only one sampling event occurred during the brood rearing period. When samples were collected on multiple dates during the brood period, we report the average of the sampling events.

Statistical Analyses

We used general linear mixed-effects models to assess the factors affecting duckling growth. We created an a priori model set using duckling mass (g) as the response variable and different combinations of duckling and habitat characteristics as explanatory variables. Model selection was performed using Akaike's Information Criterion corrected for small sample size (AICc) (Burnham and Anderson 2002). All models included the random effect of the lake and year in which the duckling was collected. These factors were combined into a single variable "Lake/Year". Due to the large number of explanatory variables, we examined fixed effects in stages in order to reduce the number of potential models in our set. The stages included covariates related to 1) duckling characteristics: sex, culmen length (mm), 2) abiotic lake characteristics: total phosphorus (TP) and lake size (LS), and 3) biomass (mg/sweep) of the most abundant aquatic invertebrate taxa. We considered all additive combinations of the covariates within stages. We restricted our models to those in which the correlation coefficient between any two covariates was <0.6 (Bausell and Li 2002). The most supported model (lowest AICc value) within a stage served as the base model for the next stage.

The first stage of our model set accounts for duckling characteristics: sex and culmen length, which would be expected to influence body mass independent of environmental conditions. We included sex in this stage as the size disparity between males and females tends to increase as

they approach fledging (Austin and Serie 1994). As we would expect, in a simple linear regression, plumage-based age class explained most of the variation in duckling mass (Adjusted R-squared=0.71, $p<0.0001$). Previous work has shown that growth rates of scaup ducklings within the range of ages we collected are essentially linear and have not yet reached asymptotic growth (Stetter 2014). However, the plumage-based age classes that we assigned to ducklings had wide ranges (from 4 to 8 days). Such an imprecise estimation of age would likely obscure significant growth variation within age classes. Alternatively, culmen length has been shown to be the best predictor of age for snow goose goslings (Cooch et al. 1999) and relatively unaffected by habitat quality for growing ducklings (Rattner et al. 1987). Therefore, we used culmen length (mm) as a proxy for age under the assumption that it would be highly correlated with true age in ducklings. As such, we did not directly measure growth rate, but rather measured size-adjusted body mass.

The second stage of our model set examined abiotic habitat characteristics TP and LS, which may serve as indirect measures of food abundance in lakes. TP, a measure of aquatic productivity, has previously been shown to have a positive effect on duckling growth and survival, likely serving as a proxy for aquatic invertebrate abundance (Sjöberg et al. 2000). LS was included, as Lewis et al. (2015) demonstrated a positive relationship between scaup brood occupancy and lake area, possibly because larger lakes may contain more foraging habitat or higher prey densities.

The third stage of our model set examined the primary factors of interest by directly examining the effect of invertebrate food abundance (biomass) (mg/sweep) on duckling growth. We included as covariates the biomass of aquatic invertebrates that were both common in our study lakes (Lewis 2015) and known to be important diet items for scaup ducklings (DuBour 2019).

We focused our analysis on the following invertebrate groups: Amphipoda, Conchostraca, Diptera, Gastropoda, Hemiptera and Odonata. Gastropod and Hemiptera mass were highly correlated (correlation coefficient =0.7); therefore, we combined these two taxa into one factor, GasHem, in our analyses. Additionally, we considered total invertebrate biomass, which summed the above invertebrate groups, as well as several other less common yet regularly occurring taxa, to include Orders: Trichoptera, Coleoptera and Anostraca. In all, we included six covariates in this stage 1) Amp, 2) Con, 3) Dip, 4) GasHem, 5) Odo and 6) Tot.

3.5 Results

We collected 102 ducklings from 27 lakes over three seasons (43 Lake/Year combinations) of which 52% were females and 48% were males and 45 and 37% were within the plumage-based age classes 2A and 2B respectively. Duckling mass ranged from 87 to 675 g ($\bar{x}$=370g, SD=132). Culmen length ranged from 18.8 to 40.9 mm ($\bar{x}$=30.7mm, SD=4.5) and explained 79% of the variation in duckling mass ($p<0.0001$) (Fig 3-2).

Total invertebrate biomass ranged from 3.4 to 198.8 mg/sweep. Amphipods reached the highest mean (23.4) and maximum (129.9) biomass (mg) of any other invertebrate within our study; however, they also had the patchiest distribution (SD=31.5) with a significant portion of lakes containing little or no Amphipods. Odonates, Gastropods and Hemipterans made relatively moderate, yet consistent, contributions to invertebrate biomass in our study lakes. With a few exceptions, Dipteran and Conchostraca biomass was consistently low (Table 3-1).

Model Selection

In the first stage of model selection we evaluated the influence of Culmen and Sex on duckling body mass. There was overwhelming support for including Culmen as it was included in the top

two models with a cumulative weight of 1.00. While there was only minor improvement in model selection with the addition of the factor Sex (ΔAICc=0.16), it was included in our top model Mass=Culmen+Sex (ω_i=0.52) serving as the base model for the next stage. Our second stage examined the influence of water chemistry (TP) and lake size. Neither variable resulted in an improved model over the top supported base model, which contains only Culmen and Sex, (ω_i=0.44) (Table 3-2).

Our third stage examined the influence of invertebrate biomass. Amphipod mass received the strongest support compared to the other invertebrates examined. While the top supported model, Mass= Culmen + Sex + Amphipod mass, had only moderate support $\omega_{i\,i}$=0.14), of the top 15 models (cumulative ω_i =0.81), 11 included Amphipod mass (Table 3-2). In the top model, Amphipod mass had a significant positive effect on duckling body mass (β=0.57, 95% CI=0.03-1.12). However, due to the model selection uncertainty we employed a model averaging procedure. Across all the models in the set, the effect of Amphipod mass was β =0.62, 95% CI=0.07-1.18 (Fig. 3-3). Parameter estimates of the other invertebrate groups varied from similarly positive (Gastropod+Hemiptera mass: β =0.61, 95% CI= -0.56 – 1.77) to strongly negative (Diptera mass: β =-1.54, 95% CI= -6.19 – 3.11), however, all were uninformative as their 95% CI were insufficiently precise for reliable inference (Arnold 2010) (Table 3-3).

Post Hoc Amphipod Biomass Analysis

Given the support for the positive effect of Amphipod mass on duckling growth, we further explored its influence. It is reasonable to assume that the relationship between Amphipod mass and duckling mass is not linear and likely levels off well before the maximum Amphipod abundances are reached. Hence, we created a categorical variable (AmpLevel) based on the

quartile values of Amphipod mass with three levels: Low: < 1.5 mg, Medium: 1.5- 37.7 mg and High: >37.7mg. We evaluated models using AmpLevel both with and without an interaction with Culmen to account for increasing disparities in growth between rich and poor lakes, as ducklings grow older. Additionally, we considered the quadratic function of Amphipod mass. We again used AICc model selection to assess the relative support for the above-mentioned models. Both the quadratic model and the previous linear model were unsupported (ΔAICc=10.2 and 10.9 respectively; ω_i <0.00). Together, the models containing AmpLevel received strong support (cumulative ω_i =0.99) with the top model being the one without the interaction (AICc=1094.77, ω_i =0.75) (Table 3-4). Predictions based on the top model indicate that ducklings from "Low" Amphipod lakes were 67.4g (95% CI=35.1 – 99.7) and 74.4g (95% CI=36.2 – 112.6) lighter than ducklings from "Medium" and "High" Amphipod lakes respectively (Fig 3-4).

3.6 Discussion

Due to prolonged population declines, scaup are considered a species of conservation concern under the North American Waterfowl Management Plan. Although the exact cause and extent of their decline is uncertain, habitat conditions on the boreal breeding grounds, including aquatic foodweb dynamics, have been identified as a research priority by the Scaup Action Team (Austin et al. 2006). Our study addressed key information gaps regarding the growth response of scaup ducklings, a generalist consumer, to variation in food resources across an important breeding area, the Yukon Flats. We found that despite their diverse diet, Amphipod abundance is the primary factor affecting mass gain for scaup ducklings in our study lakes.

Our finding that scaup duckling growth is related to invertebrate abundance is consistent with numerous previous studies across a range of species and habitats. For example, our results

confirm those of Cox et al. (1998) which demonstrated that growth and survival of mallard ducklings in experimental is ponds strongly influenced by the total number of invertebrates. Similarly, Sjöberg et al. (2000) documented that mallard ducklings reared on less productive lakes, as indexed by total phosphorus concentration (TP), experienced poor growth. However, our robust data set of invertebrate abundance enabled us to examine the influence of multiple invertebrate taxa on scaup duckling growth. Furthermore, by using natural gradients in invertebrate abundance across the landscape we demonstrated that lakes occupied by scaup broods in an arguably pristine boreal forest ecosystem vary in their quality for rearing ducklings. This is consistent with research from Fennoscandia which indicates that a large proportion of boreal lakes lack enough food to support duckling growth (Sjöberg et al. 2000, Gunnarsson et al. 2004, Nummi et al. 2013).

Our model selection results indicated that lake size (LS) and TP concentration are poor indicators of food availability for scaup ducklings as we found no support for their inclusion in our final model. We included LS in our models as Lewis et al. (2015) demonstrated that scaup broods tend to occupy relatively larger water bodies within the region. However, this relationship was likely related to the higher prevalence of Amphipods in larger lakes (Lewis et al. 2015). Our negative results for TP contrast with those of Sjöberg et al. (2000). This may be due to the relatively high productivity of Yukon Flats lakes. Sjöberg et al. (2000) defined high productivity as lakes with TP concentrations between 19-30 µg/l while TP concentration among lakes in our study was nearly ten-fold higher ($\bar{x}$=273 µg/l, SD=647µg/l). At such high concentrations, the response of invertebrate populations to variation in TP is likely dampened. Additionally, emerging chironomids, the primary food source for mallard ducklings, may be more responsive to TP concentration than the prey most important for scaup. Indeed, Chironomid abundance in our

study was strongly and positively correlated with TP (0.88) while Amphipod abundance was not (0.21).

Of the invertebrates considered, Amphipods were the only taxa that significantly influenced duckling growth in our study. The positive effect of Amphipod abundance confirms our predictions and is consistent with their previously indicated importance for scaup duckling diet (Bartonek and Murdy 1970, Gurney et al. 2017) and brood habitat use (Fast et al. 2004, Lewis et al. 2015, Gurney et al. 2017). However, we did not expect that no other invertebrate taxa (Diptera, Gatropoda, Hemiptera, Odonata and Conchostraca) would have a significant relationship with duckling mass given the variability and width of the trophic niche of scaup ducklings (Gurney et al. 2017, DuBour 2019). Furthermore, our analysis suggests a negative relationship between duckling mass and Conchostraca, Diptera and Odonata abundance. Although ducklings consume and can subsist on alternative prey, our results suggest that Amphipods offer some advantage resulting in higher growth rates. While the macro-nutrient and energetic content of Amphipods is comparable to that of other common diet items (Sugden 1973), perhaps a combination of high density, conspicuous behavior and short handling time make them a highly profitable diet item.

On average, ducklings were 0.57 grams heavier for every additional 1 mg increase in Amphipod biomass. This translated into a 74.4g difference between ducklings reared on lakes with the highest Amphipod abundances when compared to those encountering no Amphipods. However, the impact of Amphipods is not constant across the range of biomass found in our study system as demonstrated in our exploratory analysis. When grouping lakes into three levels of Amphipod biomass, we observed lower body mass in ducklings from lakes with the lowest Amphipod abundance compared to ducklings from lakes with medium and high Amphipod biomass.

However, when comparing duckling body mass from lakes with medium Amphipod biomass to lakes with high Amphipod biomass, the difference was negligible. This contrast suggests that there is a point of diminishing returns at which increasing levels of Amphipod abundance no longer results in positive gains in duckling mass. The exact point of diminishing returns is unclear given the limitations of the current analysis; however, it appears that lakes fall into two categories from the perspective of foraging scaup ducklings; those with and those without adequate Amphipod populations. Future research should attempt to identify the minimum thresholds of Amphipod abundance necessary for optimal duckling growth.

Beyond growth of individual ducklings, the abundance of food resources may have other benefits for scaup. For example, common goldeneye (*Bucephala clangula*), hereafter goldeneye, hens are territorial and will defend brood rearing habitat (Eadie et al. 1995). Nummi et al. (2015) documented that goldeneye brood occupancy was density dependent in relation to per capita food availability in Fennoscandian boreal lakes. While we did not examine such a relationship for scaup in this study it is possible that lakes with high Amphipod abundance may reduce competition among broods, thereby allowing for higher brood densities.

Limitations and Future Research

The reduced growth experienced by scaup associated with low Amphipod abundance could influence individual survival and reproductive fitness and ultimately reduce recruitment from the region. Estimates of recruitment rates by Walker and Lindberg (2005) for scaup breeding in the Minto flats of Alaska were as low as 1%. However, it remains to be determined if the reduction in body mass that we observed among scaup in lakes without Amphipods is enough to affect individual fitness or for that matter if the proportion of impacted individuals might lead to

reduced recruitment from the Yukon Flats. Subsequent studies investigating the connection between reduced growth and life history parameters, such as first-year survival and reproductive success, could provide evidence for conservation efforts to protect high quality habitat.

Our inferences are limited by our inability to precisely age ducklings (Austin and Serie 1994). We used culmen length as a proxy for age and thus were measuring size-adjusted body mass. Although culmen length has been shown to be a relatively well conserved trait under conditions of variable nutrition (Rattner et al. 1987, Cooch et al. 1999), there is the potential that our results could be biased if this assumption does not hold true. Even so, our results would still show that for ducklings of similar structural size, if not the same age, body mass is lower when they are reared on lakes without adequate Amphipod abundance. This finding would still indicate variation in growth patterns across a natural gradient in habitat quality.

There are other potential biases in our analyses. We used a coarse measurement, total body mass, as our response variable to assess growth of ducklings. By doing so, we may have overlooked more nuanced metrics. When resources are limited, individuals may selectively prioritize the development of certain physiological characteristics over others with implications for fitness. For example, Gurney et al. (2012) documented that relatively late-hatched scaup ducklings, facing potential seasonal declines in food quantity or quality, may prioritize nutrient absorption over long-term foraging efficiency by growing relatively larger digestive system organs at the expense of leg muscle growth. Additionally, as a late nesting species, scaup face considerable selective pressure to attain flight at a relatively young age (Lightbody and Ankney 1984) and may prioritize the development of flight muscles and feathers over total mass. Therefore, increasing total body mass may not be the most advantageous strategy under every condition.

Drever et al. (2011) proposed that scaup might be vulnerable to a temporal mismatch with their invertebrate prey because of a changing climate. However, in examining the impact of heterogeneity in food resources, logistical constraints required that we prioritize spatial and inter-annual variation over intra-seasonal variation. Therefore, we were unable to make robust estimates of the seasonal trends in invertebrate abundance that would be necessary to investigate the potential for a trophic mismatch for scaup ducklings. Future studies should investigate duckling growth in relation to the timing of peaks in invertebrate abundance, particularly Amphipods, which could provide information on scaup vulnerability to temporal shifts in food-web dynamics.

Conservation Implications

Boreal lakes are typically considered productive and high-quality habitats for breeding waterbirds (Slattery et al. 2011). However, our study demonstrates that there is variation in the quality of boreal brood-rearing habitat and that such variation influences scaup at an important stage of their life history. For scaup ducklings, an apparently generalist consumer, the abundance of one prey item (Amphipods) had an elevated impact on growth, highlighting the importance of considering fitness consequences when examining resource selection in animals.

Recently documented loss of lake surface area in boreal Alaska (Riordan et al. 2006) and the concurrent decline in Amphipod abundance (Corcoran et al. 2009, Lewis et al. 2016) should be a concern for wildlife managers given the effect of Amphipod abundance on scaup growth demonstrated here. Previous work in Alaskan and Canadian boreal habitats have highlighted the importance of Amphipods as a predictor of habitat use by scaup and other species such as white-winged scoter (*Melanitta deglandi*) (Haszard and Clark 2007, Lewis et al. 2015, Gurney et al.

2017). The YFNWR and other land managers should prioritize the conservation of boreal lakes that contain Amphipods. However, our results suggest that even lakes with relatively low Amphipod populations are valuable habitat for scaup broods, providing managers with an efficient means to assess habitat quality based on the presence of Amphipods.

3.7 Acknowledgements

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3.9 Figures

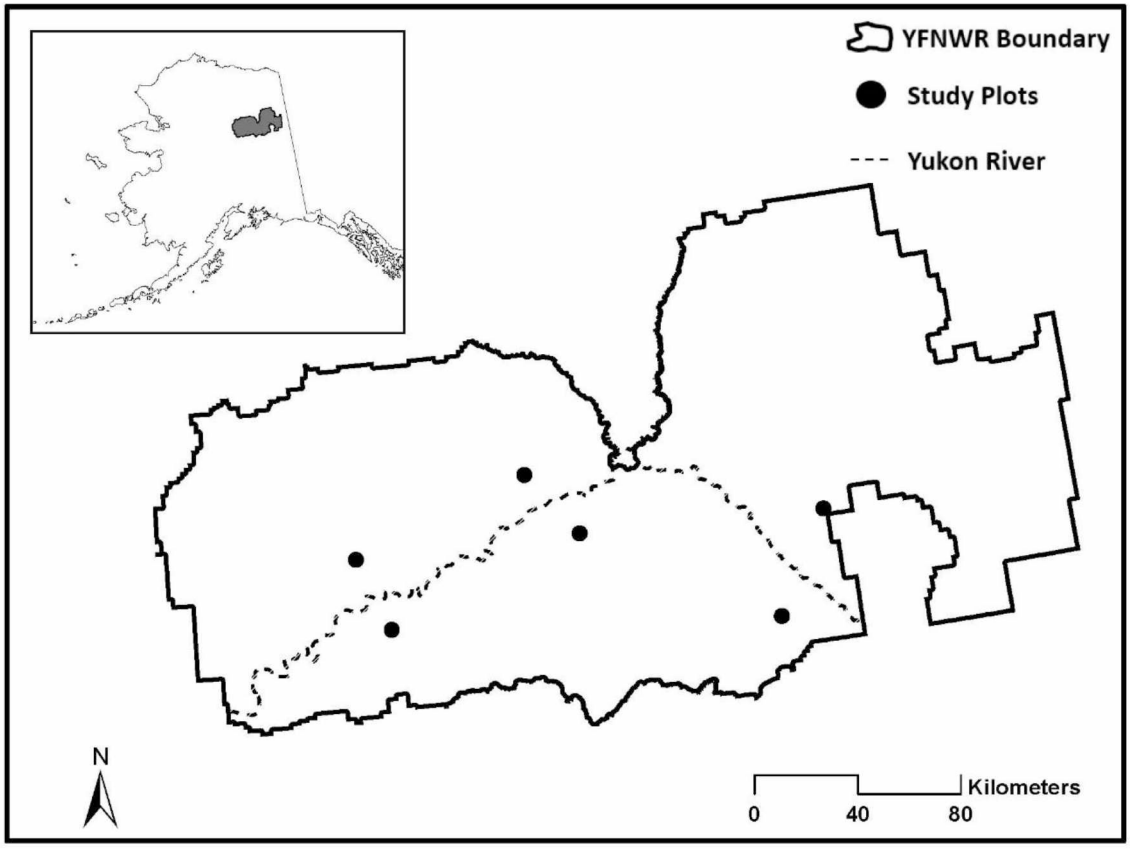

Figure 3-1. Map of the Yukon Flats National Wildlife Refuge study area with the six plots depicted by the black circles. The Yukon River, depicted by a dashed line, bisects the study area with three plots to the north and three plots to the south. The general location of the Yukon Flats National Wildlife Refuge within Alaska is depicted in the inset.

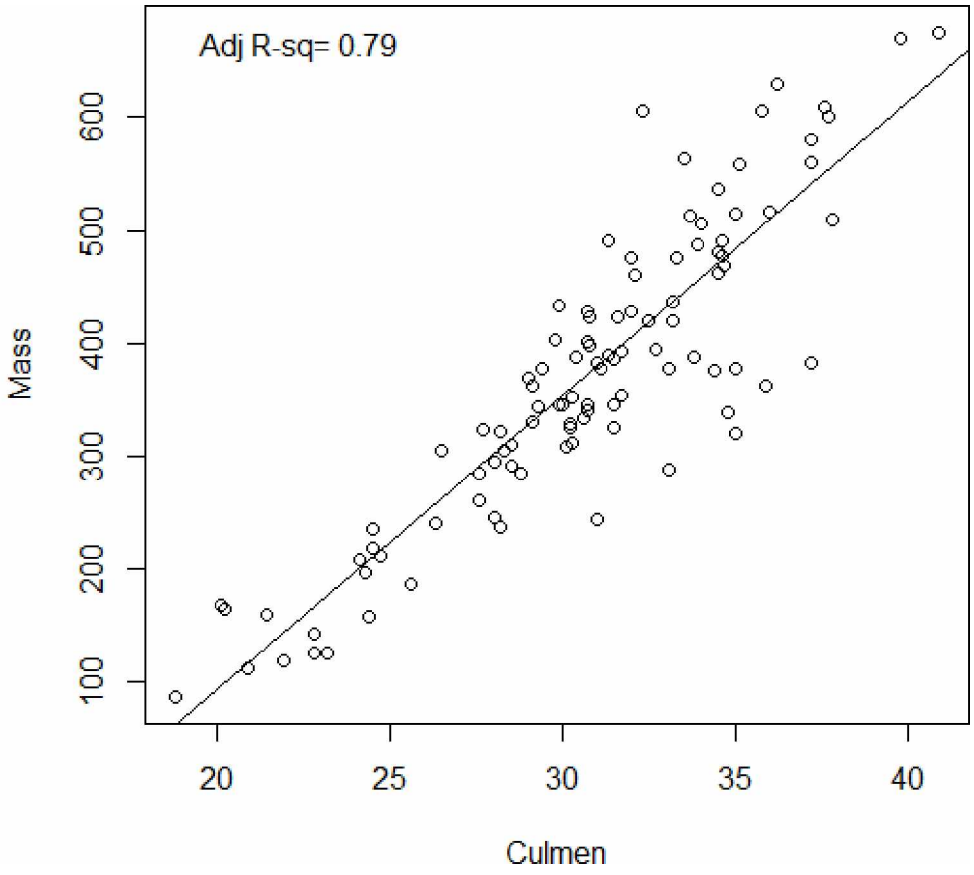

Figure 3-2. In a simple linear regression, culmen length (mm) explains 79% of the variation in duckling mass (g).

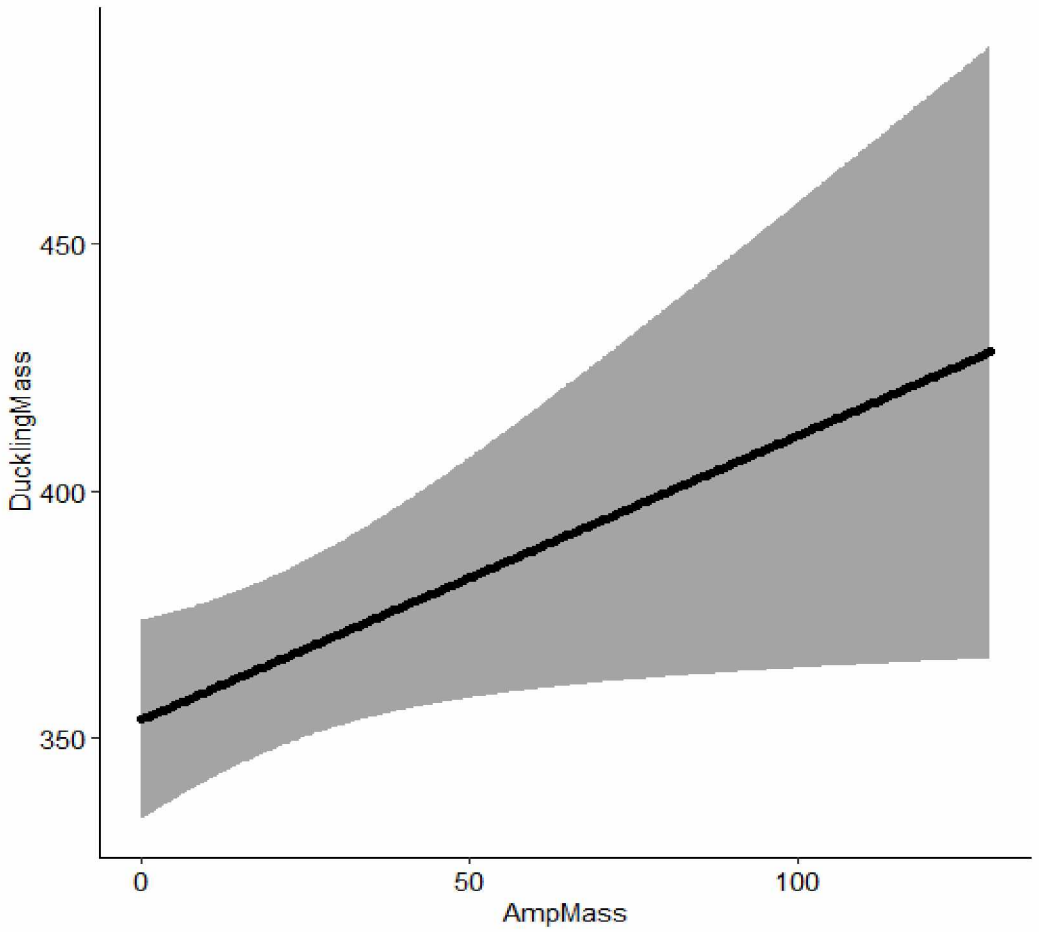

Figure 3-3. Model predicted estimates of duckling mass (g) across the range of observed amphipod mass (mg/sweep). Grey band depicts 95% confidence interval of the model-based estimate.

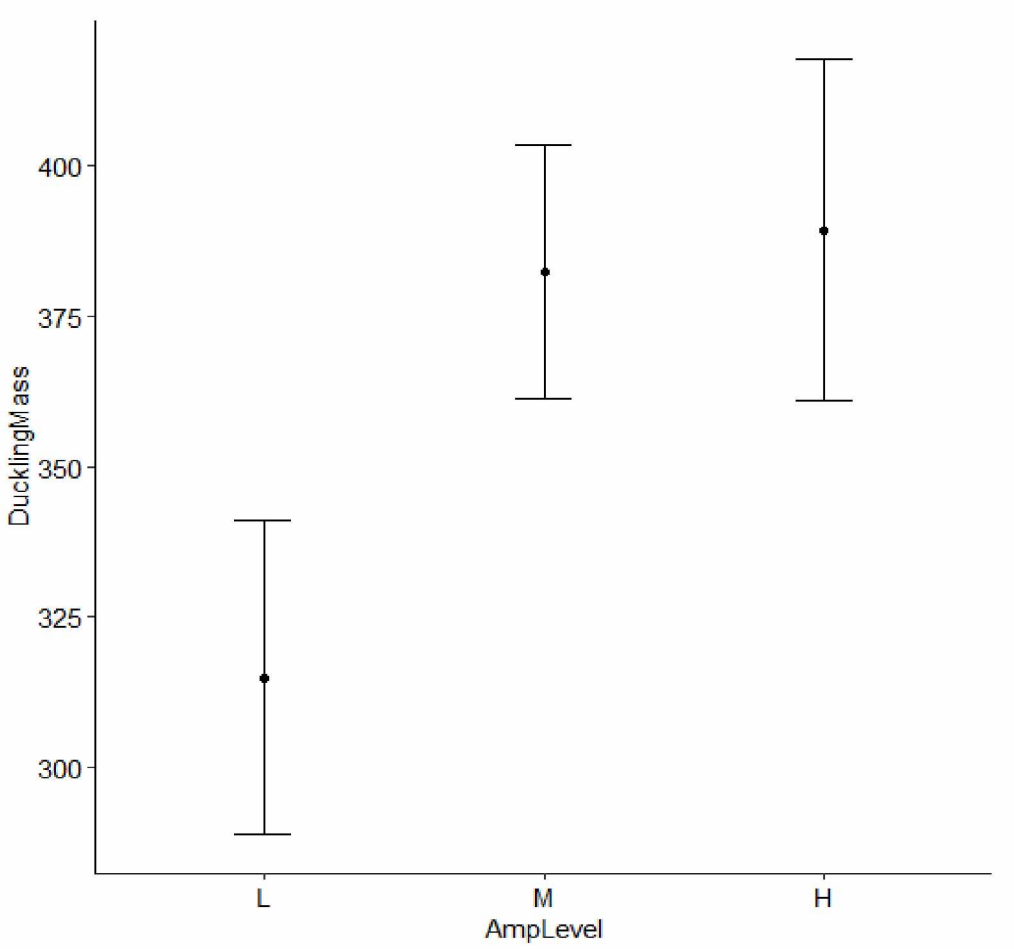

Figure 3-4. Duckling mass (g) among three categories of lakes based on average amphipod mass (mg/sweep). Low= 0 -1.5 mg; Medium=1.5-37 mg and High= 37-130 mg, n=26, n=46 and n=30, respectively. Error bars represent 95% confidence intervals. Ducklings from Low amphipod lakes are significantly lighter.

3.10 Tables

Table 3-1. Summary statistics for the invertebrate biomass covariates used in our model set. Values represent the average dry mass in mg per sweep for Amphipoda, Conchostraca, Diptera, Gastropoda, Hemiptera, Odonata and an additional covariate, Total, which includes Coleoptera, Trichoptera and Anostraca in addition to the previous invertebrate groups.

Invertebrate Biomass (mg/sweep)	Min	Quartile 1	Median	Quartile 3	Max	SD
Amphipod	0	1.48	6.99	37.7	129.88	31.48
Conchostraca	0	0.07	0.67	3.37	19.07	4.41
Diptera	0.01	0.56	0.95	2.31	21.01	4.42
Gastropoda	0.05	3.64	6.52	12.44	46.75	9.4
Hemiptera	0	1.52	3.33	4.69	43.35	8.37
Odonata	0.27	4.65	9.96	19.87	45.76	10.96
Total	3.41	30.76	53.85	75.68	198.82	48.47

Table 3-2. Ranking of top mixed effects models explaining the variation in scaup duckling mass. Models were considered in three stages with covariates related to 1) Duckling characterisitcs: Culmen and Sex; 2) Lake characteristics: LS=a three level factor based on lake surface area and TP=Total Phosphorous concentration (µg/l); and 3) Invertebrate biomass (mg/sweep): Amp=Amphipoda, Con=Conchostraca, Dip=Diptera, GasHem=Gastropoda+Hemiptera, Odo=Odonata and Tot=Coleoptera, Trichoptera and Anostraca + the previous five groups. Models are ranked using Akaike's information criterion, corrected for small sample size (AIC_c). K=Number of parameters within a model. ω_i =AIC_c weight. Cumulative ω_i refers to the summed ω_i within a stage. In stage three we only report the top 15 out 33 models in which $\Delta AIC_c \leq 4.00$.

Model	ΔAIC_c	K	ω_i	Cumulative ω_i
Stage 3: Invertebrate Biomass				
Culmen+Sex+Amp	0	6	0.14	0.14
Culmen+Sex+Amp+Odo	0.41	7	0.12	0.26
Culmen+Sex+Amp+GasHem+Odo	1.23	8	0.08	0.34
Culmen+Sex+Amp+Dip	1.69	7	0.06	0.40
Cumenl+Sex	1.97	5	0.05	0.46
Culmen+Sex+Amp+GasHem	2.03	7	0.05	0.51
Culmen+Sex+Tot	2.09	6	0.05	0.56
Culmen+Sex+Amp+Con	2.28	7	0.05	0.61
Culmen+Sex+Amp+Dip+Odo	2.63	8	0.04	0.65
Culmen+Sex+Amp+Con+Odo	2.66	8	0.04	0.68
Culmen+Sex+GasHem	3.29	6	0.03	0.71
Culmen+Sex+Amp+GasHem+Dip+Odo	3.34	9	0.03	0.74
Culmen+Sex+Amp+GasHem+Dip	3.49	8	0.03	0.77
Culmen+Sex+Amp+GasHem+Con+Odo	3.50	9	0.03	0.79
Culmen+Sex+Odo	3.85	6	0.02	0.81
Stage 2: Lake Characteristics				
Culmen+Sex	0.00	5	0.44	0.44
Culmen+Sex+LS	0.85	7	0.29	0.72
Culmen+Sex+TP	2.12	6	0.15	0.88
Culmen+Sex+TP+LS	2.54	8	0.12	1.00
Stage 1: Duckling Characteristics				
Culmen+Sex	0.00	5	0.52	0.52
Culmen	0.16	4	0.48	1.00
Intercept	172.45	3	0.00	1.00
Sex	174.34	4	0.00	1.00

Table 3-3. Model-averaged parameter estimates, unconditional standard errors and 95% confidence intervals from the third stage of models evaluating scaup duckling growth. Covariates include the average biomass (mg) per sweep of six invertebrate categories: Amp=Amphipoda, Con=Conchostraca, Dip=Diptera, GasHem=Gastropoda + Hemiptera, Odo= Odonata and Tot=Coleoptera, Trichoptera and Anostraca + the previous five groups.

Covariate	Estimate	SE	95% Confidence Interval
Amp	0.62	0.28	0.07 – 1.18
Con	-0.62	1.99	-4.51 – 3.27
Dip	-1.54	2.37	-6.19 – 3.11
GasHem	0.61	0.59	-0.56 – 1.77
Odo	-1.12	0.83	-2.75 – 0.5
Tot	0.26	0.18	-0.08 – 0.6

Table 3-4. Comparison of the top supported model explaining the variation in scaup duckling mass containing amphipod mass as a continuous covariate (Amp) with models including the quadratic function (Amp^2), amphipod mass as a three-level categorical covariate (AmpLevel) and an interaction between AmpLevel and Culmen. Models are ranked using Akaike's information criterion, corrected for small sample size (AIC_c). K=Number of parameters within a model. ω_i =AIC_c weight.

Model	ΔAIC_c	K	ω_i	Cumulative ω_i
Culmen+Sex+AmpLevel	0.00	7	0.75	0.75
Culmen+Sex+AmpLevel*Culmen	2.30	9	0.24	0.99
Culmen+Sex+Amp^2	10.22	7	0.00	1.00
Culmen+Sex+Amp	10.91	6	0.00	1.00

Chapter 4 General Conclusions

Following several decades of declines and a limited subsequent recovery, scaup populations are still 20% below the long-term average (USFWS 2018). Despite extensive investigations, researchers and managers have been unable to reach a consensus regarding the underlying cause (Afton and Anderson 2001, Arnold et al. 2016, Lindberg et al. 2017). While several non-mutually exclusive hypotheses have been put forward, the impetus for this study was the implication that changes to boreal breeding habitats may have played a role in declines (Austin et al. 2014). There is in fact ample evidence of dramatic changes to boreal habitats in recent decades (Riordan et al. 2006), including changes to populations of aquatic invertebrates that are considered key prey items for scaup ducklings (Corcoran et al. 2009, Lewis et al. 2016). Specifically, Drever et al. (2011) proposed that a warming climate has resulted in temporal shifts in the life history of the primary aquatic invertebrate prey of scaup ducklings, resulting in a trophic mismatch. However, there is uncertainty regarding how scaup ducklings might respond to changes in prey availability. In this study, I addressed that uncertainty to fill in key information gaps regarding the feeding ecology of scaup ducklings.

I examined the trophic niche (Chapter 2) and growth (Chapter 3) of scaup ducklings, and the variation of these characteristics across a large-scale heterogeneous wetland system. The lakes that I sampled in the Yukon Flats National Wildlife Refuge had variable compositions and abundances of aquatic invertebrates, which are commonly consumed by scaup ducklings (Lewis 2015). Amphipods are generally cited as the primary prey of scaup. On lakes used by scaup in the YFNWR, Amphipods reached higher densities than other invertebrates, yet had the most variable distributions (Lewis et al. 2015). This natural variation, along with that of other

invertebrates, presented an ideal system in which to make inferences about how spatial or temporal changes to aquatic invertebrates might affect scaup.

In Chapter 2, I used a stable isotope approach to examine the overall tropic niche of scaup ducklings, the patterns of variation in the population niche and the ecological causes of such variation (Semmens et al. 2009). In addition to addressing issues relevant to scaup conservation and management, I also contributed to the broad ecological knowledge of the causes of Intra-population niche variation (IPNV) as described by Bolnick et al. (2003). Both traditional gut content analysis and the Bayesian stable isotope mixing model that I employed found that scaup ducklings at the population level have a relatively broad trophic niche. While these results suggest that Amphipods are a common prey item, scaup duckling diet is characterized by the consumption of various crustaceans, gastropods and aquatic insects. This comports well with what others have documented for scaup duckling diet (Bartonek and Murdy 1970, Sugden 1973, Gurney et al. 2017). The hierarchical nature of MixSIAR, allowed me to partition diet among several population levels. I found that "Lake" was the factor that most contributed to variation in the population diet. Individuals from the same lake, which presumably had access to the same resources, had diets that were more similar as compared to individuals from other lakes. Gurney et al. (2017) similarly found that variation in invertebrate biomass associated with habitat heterogeneity was a strong driver of scaup niche variation.

A more holistic understanding of scaup duckling vulnerability requires an examination of fitness consequences associated with changes in their food sources as well. Therefore, in Chapter 3, I explored the variation in duckling growth in relation to invertebrate biomass by again taking advantage of the natural variation in invertebrate populations found across lakes in the study area. Of all the invertebrate and habitat factors that I examined, only Amphipod biomass had a

significant impact on duckling mass. Ducklings from lakes with little or no Amphipods were significantly lighter than ducklings from lakes with even moderate Amphipod densities. However, this study was unable to determine the minimum threshold of Amphipod density. These results confirm those that highlight the importance of invertebrate abundance for duckling growth (Cox et al. 1998).

The results from Chapters 2 and 3 somewhat contradict one another. On the one hand, in Chapter 2, I found that scaup ducklings are a generalist consumer that appear able to adapt to changes in food resources. On the other hand, while ducklings can subsist on a variety of prey other than Amphipods, my results from Chapter 3 suggest that the use of alternative prey may negatively influence growth. Optimal foraging theory predicts that animals will select the most profitable prey (Stephens and Krebs 1986). However, ducklings may be naïve predators unable to assess prey profitability or simply cannot dive well enough to capture their preferred prey efficiently. This assumption is supported by the observation of ducklings increasing the proportion of Amphipods in their diet as they age (Sugden 1973). Therefore, the burden of ensuring that ducklings consume the most optimal diet falls on the hens when selecting brood rearing habitat. This is supported by the observation that scaup broods disproportionately occupy habitats that contain Amphipods (Lewis et al. 2015, Gurney et al. 2017). Presumably, the more experienced or higher quality hens are more successful at selecting brood rearing habitat that provide their ducklings with access to Amphipods.

While this study does not claim to resolve the uncertainty surrounding the causes of scaup population declines, it addresses fundamental questions about the feeding ecology of scaup ducklings. Overall, my research suggests that despite an adaptable diet, scaup ducklings experience benefits from consuming Amphipods. However, the question remains if fitness, either

immediate survival or lifetime reproductive success, varies across this heterogeneous landscape in the same way that diet and growth do. Additionally, it is still unclear how Amphipods will respond to further climate related changes in boreal aquatic habitats. Future research should attempt to address these questions. Regardless of this uncertainty, this research lends further support to the evidence that lakes with Amphipods are important for scaup and should be conserved. Furthermore, my research highlights the importance of considering intra-population variation when evaluating how animals respond to their environments.

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Appendix

Values derived from the literature for the constants *a* and *b* used in the equation, lnDM= ln*a* + *b* lnL, to estimate invertebrate mass (mg) from length (mm) measurements. References are indicated by the superscript lower-case number (1-5) after the invertebrate taxa name. The values for Crustacea were used for Conchostraca, Cladocera and Ostrocoda.

	a	***b***
Amphipoda[1]	0.0058	3.015
Coleoptera[1]	0.0077	2.91
Crustacea[2]	0.0138	2.669
Diptera[1]	0.0025	2.692
Ephemeroptera[1]	0.0071	2.832
Gastropoda[3]	0.00874	3.21
Hemiptera[1]	0.0108	2.734
Hymenoptera[4]	0.56	1.56
Odonata[1]	0.0078	2.792
Oligochaete[5]	0.0001	3.25
Trichoptera[1]	0.0056	2.839

References: [1]Benke et al. 1999; [2]Gruner 2003; [3]Baumgärtner and Rothhaupt 2003; [4]Sabo et al. 2002; [5]Miserendino 2001